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Revision of the family Chrysopolomidae Aurivillius, 1895 (Lepidoptera: Zygaenoidea) with the description of three new genera

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urn:lsid:zoobank.org:author:BA99CAC4-1D86-4F31-8567-984C45419A92

Abstract. The taxonomy and nomenclature of the small Afrotropical family Chrysopolomidae Aurivillius, 1895 is updated utilising a holistic approach incorporating genetic and morphological evidence. The placement of genera within the two subfamilies erected by Hering (1937), Chrysopolominae and Ectropinae, is clarified, the generic boundaries are defined and a list of all known taxa is provided. Based on phylogenetic and morphological results, two new genera of Ectropinae are described: *Muscectropa* gen. n. and *Pseudectropona* gen. n. *Achrocerides* Hering, 1937, *Strigivenifera* Hering, 1937 and *Diquishia* Kurshakov & Zolotuhin, 2016 are transferred out of Ectropinae and back into Chrysopolominae, the *Chrysopoloma* species *C. restricta* Distant, 1899 is transferred to *Scotinocerides*, and three *Hamartia* taxa *H. medora moulini* Rougeot, 1977, *H. paupera paupera* (Hering, 1937) and *H. paupera johanni* Rougeot, 1977 are transferred to *Chrysopoloma*. In addition, a new genus for *S. nigrociliata* is established based on genital morphology and genetic divergences: *Auripoloma* gen. n. Genitalia figures accompany re-descriptions of each genus and a key to the genera is provided to facilitate identifications.

Key words. Taxonomy, phylogenetics, Afrotropics, subfamily.

INTRODUCTION

Chrysopolomidae Aurivillius, 1895 is a small poorly-studied family of uniquely Afrotropical moths currently containing twelve genera (Hering 1937; Kurshakov & Zolotuhin 2016). They are considered to be sister to the Limacodidae + Dalceridae based on recent phylogenetic reconstructions (Mayer et al. 2021) and share similar wing venation as well as larval and pupal stages (Aurivillius 1895; Hering 1937; Epstein 1996), although a few species of Eupterotidae and Lasiocampidae have mistakenly been associated with the family due to similarities in external appearance (e.g., Druce 1886). Chrysopolomidae species are small to medium in size, often beige or light brown in colour with broad, rounded wings and bipectinate antennae and many species also possess a discal spot on the forewing. The family is most species-rich in southern Africa (Hering 1937), although their range extends through Central and West Africa, as well as to Madagascar where a monotypic genus is present.

Hering (1937) revised the entire family in detail introducing two subfamilies, Chrysopolominae and Ectropinae, and described several new genera and a number of new species. Kurshakov & Zolotuhin (2013a) later believed that Hering's division into two subfamilies was "not complete" and that the generic placements were incorrect although no formal changes were made to rectify this.

Epstein (1996) had considered Chrysopolomidae to be a subfamily of Limacodidae due to observed synapomorphies in several stages of the life cycle including stemma 5 being proximate to stemma 4 in the larvae, the hard, oval cocoon with no visible 'lid' prior to eclosion, and the presence of pretarsal pads and lateral lobes on the 8th segment of adult females. Based on differences in the male genital musculature as well as the absence of a frenulum in Chrysopolomidae (which is present in Limacodidae), Zolotuhin et al. (2014) firmly concluded that they were distinct families. Two recent molecular studies that included Chrysopolomidae genera placed the family within the limacodid group (sensu Epstein 1996) but its position within this group has differed. Zaspel et al. (2015) utilised three genetic markers as part of investigations into the evolution of larval traits in the Limacodidae, which resulted in 'Chrysopolominae' being nested within Limacodidae, and Dalceridae + *Pantoctenia* Felder, 1874 forming a sister-group. In the most recent multi-gene analysis of Lepidoptera (Mayer et al. 2021), Chrysopolomidae was recovered in a highly-supported clade as sister to Limacodidae + Dalceridae, with the authors conclud-

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ing that either Chrysopolomidae should be treated as a family or Dalceridae be treated as a subfamily. Although it has been suggested that further research may support the inclusion of Dalceridae within Limacodidae (Epstein 1996), both Zaspel et al. (2015) and Mayer et al. (2021) treat is as a family and thus following the results of Mayer et al. (2021), Chrysopolomidae is herein maintained as a family.

In the most recent review of the Chrysopolomidae by Zolotuhin et al. (2014), the placement of genera within the subfamilies was investigated through examination of the muscle morphology of the male genitalia. Originally, Hering (1937) assigned two tribes within Chrysopolominae based on the numbers of spurs on the hindtibia, comprised of the following genera: Achroceridini (*Achrocerides* Hering, 1937 and *Scotinocerides* Hering, 1937) and Chrysopolomini (*Chrysopoloma* Druce, 1886, *Strigivenifera* Hering, 1937, *Hamartia* Hering, 1937 and *Erythropteryx* Hering, 1937). Based on the "main morphological types" of the genitalia, Zolotuhin et al. (2014) transferred the tribe Achroceridini, which they stated to contain *Achrocerides* and *Strigivenifera* (incorrectly citing Hering (1937)), from Chrysopolominae to Ectropinae, while *Scotinocerides* was placed in the Chrysopolomini. It is clear that Zolotuhin et al. (2014) intended for *Strigivenifera* to be placed within the same tribe as *Achrocerides* due to similarities in their genitalia (e.g., the juxta is comprised of two long, distally pointed lobes). Kurshakov & Zolotuhin (2016) alluded to this later by placing their newly-described genus *Diquishia* Kurshakov & Zolotuhin, 2016 within the tribe Achroceridini while referring to similarities of the male genitalia to *Strigivenifera*.

Although Zolotuhin et al. (2014) presented a novel concept for taxonomic classification accompanied by detailed descriptions of the muscle morphology, a hitherto poorly researched topic, it cannot be overlooked that their review ignored Epstein's (1996) morphological synapomorphies and did not include any additional taxonomic methods to support their conclusions. This has resulted in the incorrect placement of several genera and species within each subfamily, which are discussed further and rectified herein. The present paper aims to revise the Chrysopolomidae, clarify the placement of genera within the subfamilies and define the generic boundaries based on a combination of external and genital morphology as well as modern genetic barcoding techniques.

MATERIAL AND METHODS

Morphological studies

Images of adults were taken using a Nikon D90 camera equipped with a Nikkor AF Micro 60 mm lens. The genitalia were dissected and stained with Eosin Y applying standard methods of preparation (Lafontaine & Mikkola 1987), then embedded in Euparal on microscope slides. The genitalia preparations were photographed using a Canon EOS 700D camera mounted on a Leitz Diaplan compound microscope.

Terminology of wing venation follows Zolotuhin et al. (2013a, b) and male genital morphology follows Zolotuhin et al. (2014), wherein 'transtilla' refers to a gnathos-like structure separated from the valve. Their research suggested that the muscles m3(2) and m4 found in Chrysopolomidae are typically associated with the transtilla or basal processes of the valve, but never with the gnathos and this conclusion is followed here. An annotated diagram of the Chrysopolomidae genitalia can be found in Fig. 1.

Genetic analyses

DNA barcodes were obtained by removing tarsal segments from 128 adult specimens (one Limacodidae and 127 Chrysopolomidae) and submitting them to the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) for extraction, amplification and sequencing of cytochrome oxidase subunit I (COI-5P) applying Single Molecule Real-Time sequencing through the Sequel (PacBio) pipeline (Hebert et al. 2018). Based on the phylogenetic inference of Mayer et al. (2021), a Limacodid *Parasa carnapi* Karsch, 1899, was selected as the appropriate outgroup taxon belonging to the sister family of Chrysopolomidae. These barcodes were combined with 142 publicly available sequence data from BOLD, resulting in a dataset of 270 sequences for the phylogenetic analyses. Taxon sampling included all bar two genera in the subfamily (*Diquishia* and *Vietteopoloma* Hering, 1961 could not be sequenced) and all type species for those genera sampled: *Achrocerides*, *Chrysectropa* Bethune-Baker, 1911, *Chrysopoloma*, *Chrysopolomides* Hering, 1937, *Ectropa* Wallengren, 1863, *Ectropona* Kurshakov & Zolotuhin, 2013, *Erythropteryx*, *Hamartia*, *Scotinocerides*, and *Strigivenifera*. All sequences and metadata are accessible in the BOLD public dataset (https://doi.org/doi.org/10.5883/DS-CHRY).

Sequences were aligned using MUSCLE in MEGA ver. X (Kumar et al. 2018) and genetic divergences within and between species were calculated using the Kimura 2-parameter model (Kimura 1980). Phylogenetic tree searches were performed using Bayesian Inference (BI) and Maximum Likelihood (ML). BI analyses were performed using MrBayes ver. 3.2.7a (Ronquist et al. 2012). Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses were run with four chains (one cold and three heated) for 10,000,000 generations sampling every 100 generations, discarding the first 25% as burn-in. The two runs converged with the standard deviation of split frequencies 0.003. ML analyses were performed using RAxML on CIPRES Portal ver. 3.3 (Miller et al. 2010) with default settings and a GTR+G model. Support

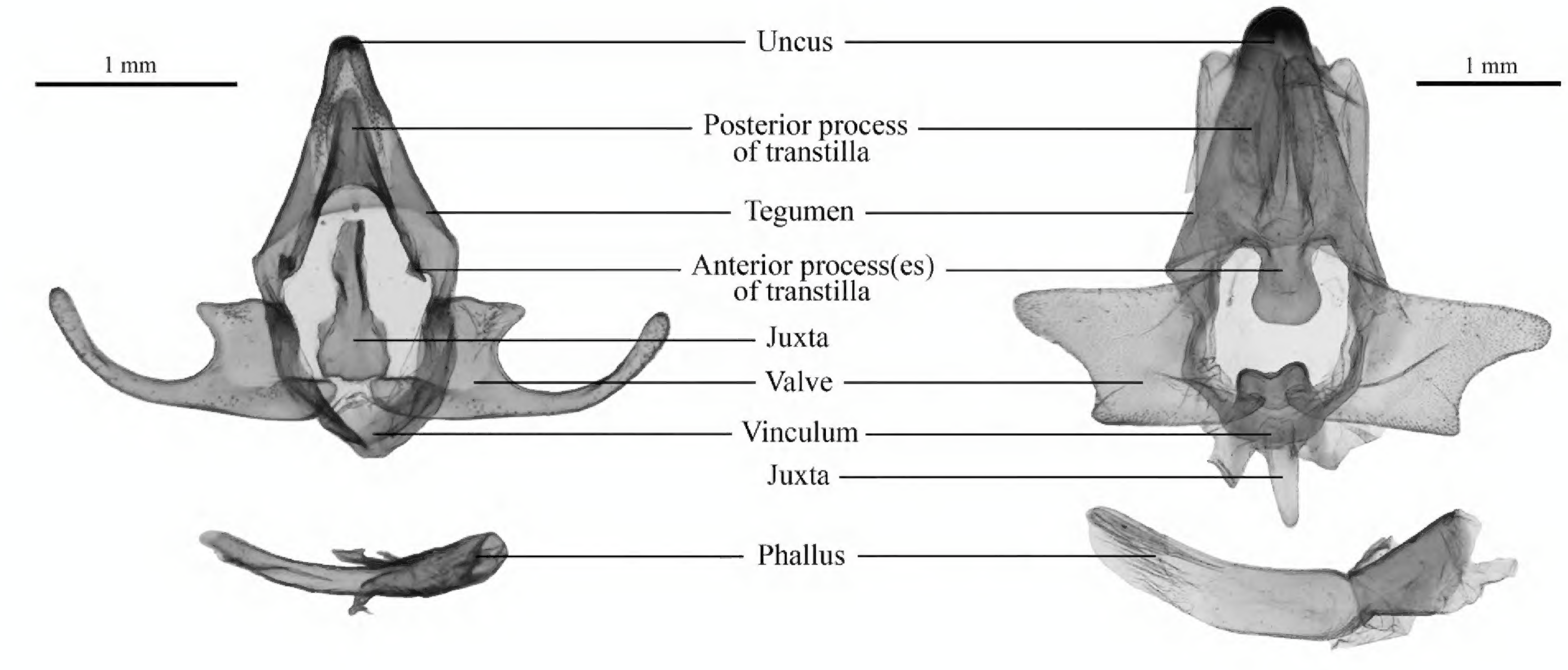

1 mm
Uncus
1 mm
Posterior process of transtilla
Tegumen
Anterior process(es) of transtilla
Juxta
Valve
Vinculum
Juxta
Phallus

Fig. 1. Terminology of Chrysopolomidae genitalia, showing representatives from subfamily Ectropinae (left) and subfamily Chrysopolominae (right).

for clades was evaluated for BI using posterior probabilities (PP) and ML using non-parametric bootstrapping (BS) with 1000 replicates. Trees were visualised and annotated in FigTree ver. 1.4.4 and Adobe Photoshop ver. 13.0.

Institutional abbreviations

ANHRT = African Natural History Research Trust, Leominster, UK
MfN = Museum für Naturkunde, Berlin, Germany
MNHN = Muséum national d'Histoire naturelle, Paris, France
MWW = Museum Witt, Weiden, Germany (former Museum Witt, Munich, Germany)
NHMUK = Natural History Museum, London, UK
RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RMCA = Royal Museum for Central Africa, Tervuren, Belgium
SMHN = Naturhistoriska Riksmuseet, Stockholm, Sweden
ZSM = Zoologische Staatssaammlung München, Munich, Germany

Other abbreviations

BOLD = Barcode of Life Data System
DRC = Democratic Republic of Congo

RESULTS

Phylogenetic analyses

The phylogenetic inferences based on BI and ML overall recovered very similar topologies, whereby there are two distinct lineages within Chrysopolomidae broadly referable to the subfamilies Ectropinae (clade A) and Chrysopolominae (clade B). The slightly better-resolved ML tree is figured in Fig. 2.

Ectropinae s.n. (Fig. 3) was recovered as monophyletic in every analysis with strong support values (BS: 93 and PP: 100) suggesting it is clearly a distinct unit reflective of Hering's (1937) original species' placements and Ectropini sensu Zolotuhin et al. (2014). *Chrysectropa* and *Chrysopolomides* were recovered as monophyletic which is supportive of the clear morphological differences in both the external habitus and genitalia. *Ectropa* was also recovered as monophyletic but with a large divergence between the two clusters (APWD=8.83±0.09%), and upon further morphological investigation, it has become apparent that one of the clusters pertained to an undescribed genus. *Ectropona* was surprisingly recovered as paraphyletic but morphological assessments confirmed the presence of a second undescribed genus. Both new genera are discussed and described under the Ectropinae section below.

The Chrysopolominae was also recovered as monophyletic in every analysis with strong support values (BS: 57 and PP: 90). All genera within the Chrysopolominae were recovered as monophyletic with the exception of *Scotinocerides* and *Hamartia* which were recovered as polyphyletic. Within the subfamily, two distinct lineages were identified, clade C (*Chrysopoloma*, *Scotinocerides* (partim), *Hamartia*, *Erythropteryx*, and *Strigivenifera*) and clade D (*S. nigrociliata* and *Achrocerides*). The overall largest clade (in terms of taxa) existed within clade C, herein referred to as clade E, containing *Scotinocerides* (partim), *Chrysopoloma* and *Hamartia* (partim). Within this clade, two distinct lineages were recovered in both analyses herein referred to as the ‘line’ and ‘spot’ clades (note: this feature is only applicable to males). Species in the ‘line’ clade (referable to *Scotinocerides*) are typically larger and often have a postmedial line on the forewing. It must be noted that this appears to be variable; for example, a specimen with a line (ANLMN8388-21) clustered as identical in DNA barcodes to a specimen without a line (ANLMN8386-21) although this is unsurprising given the known intraspecific variation in external morphology in the Chrysopolomidae (e.g., Taberer 2022).

Species recovered in the ‘spot’ clade (referable to *Chrysopoloma*) possess a small discal spot on the forewing, sometimes appearing only very faintly, whilst they are also typically smaller in size than those of the ‘line’

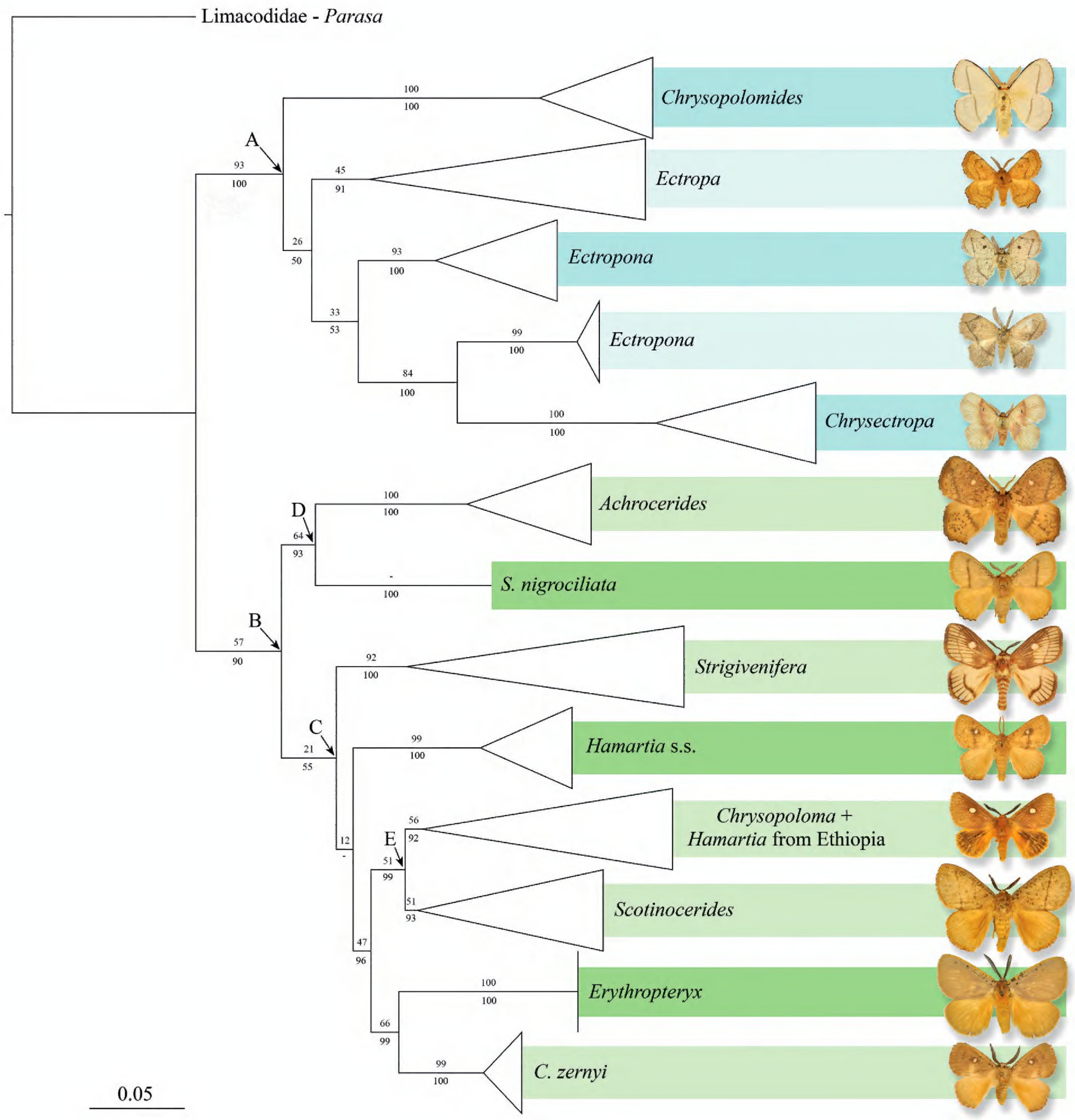
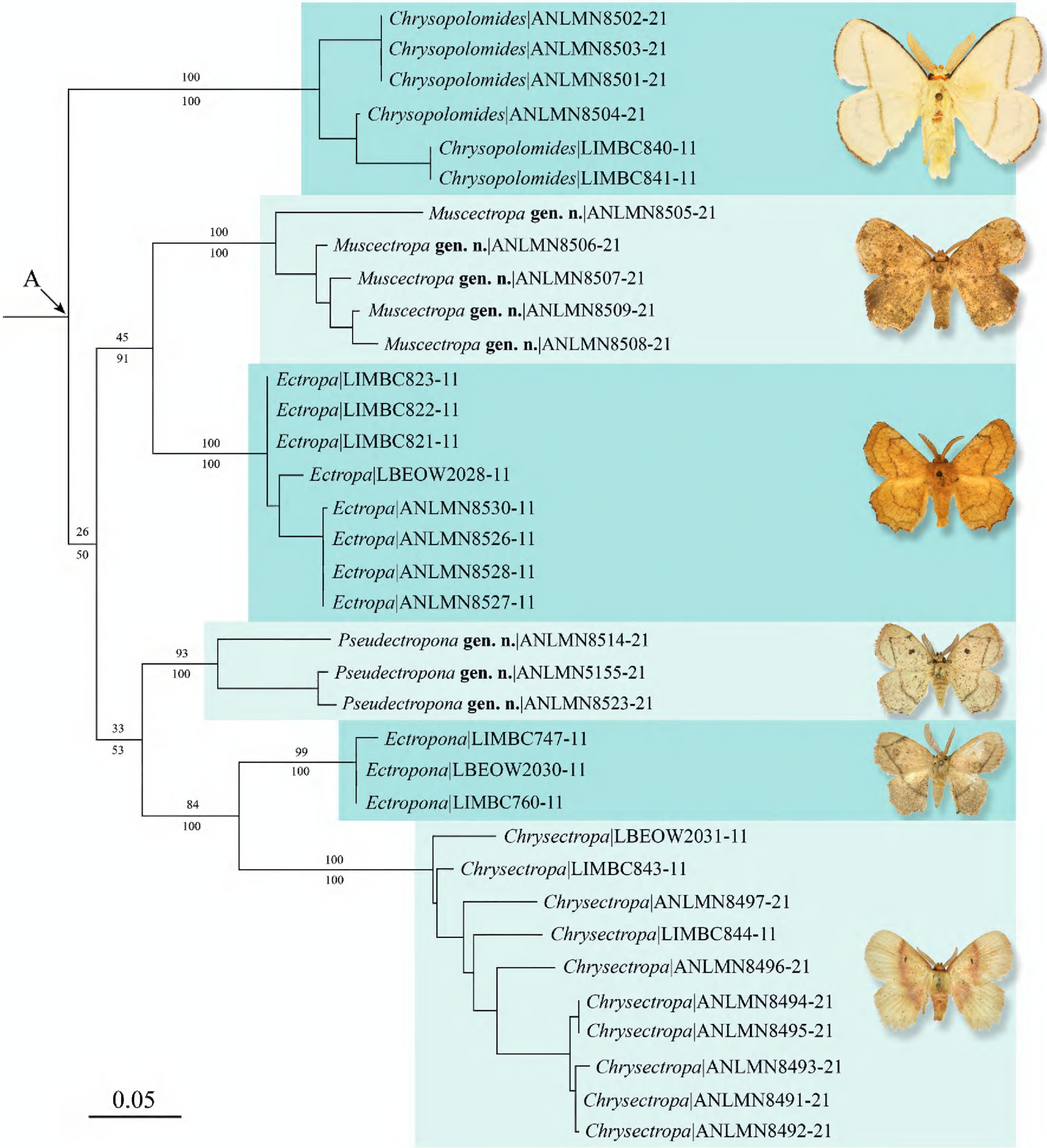


Fig. 2. Phylogenetic tree (Maximum-Likelihood, generated by RAxML from complete sequences of 658 bp CO1-5P obtained in BOLD) of the family Chrysopolomidae with 234 Chrysopolominae and 35 Ectropinae specimens, and a representative outgroup in the family Limacodidae. Posterior probabilities and bootstrap values are provided above and below the branches respectively.

lineage. Interestingly, *Chrysopoloma rudis* (the type species of *Chrysopoloma*) which possesses both a forewing discal spot and a continuous diffuse line on both wings was recovered as sister to all other 'spot' taxa. Part of the sampled *Hamartia* (those taxa from Ethiopia) were recovered within this 'spot' cluster, some specimens also possessing a line on the forewing (e.g., LBEOW2062-11) whilst others do not (e.g., LBEOW2059-11). The recovery of *Hamartia* as a polyphyly was considered surprising at first given these moths are extremely similar in external habitus. However, genitalia dissections revealed that these *Hamartia* taxa from Ethiopia share the typical features of *Chrysopoloma* such as the broad gnathos comprised of two laterally fused lobes as well as the juxta comprising a central process and two lateral processes, and have thus been misplaced. Overall, all members of clade E share very similar genital morphology groundplans, however, the clear partitioning of *Scotinocerides* from *Chrysopoloma*, in combination with distinctive



Chrysopolomides|ANLMN8502-21
Chrysopolomides|ANLMN8503-21
Chrysopolomides|ANLMN8501-21
100
100
Chrysopolomides|ANLMN8504-21
Chrysopolomides|LIMBC840-11
Chrysopolomides|LIMBC841-11
Muscectropa gen. n.|ANLMN8505-21
100
100
Muscectropa gen. n.|ANLMN8506-21
A
Muscectropa gen. n.|ANLMN8507-21
Muscectropa gen. n.|ANLMN8509-21
45
91
Muscectropa gen. n.|ANLMN8508-21
Ectropa|LIMBC823-11
Ectropa|LIMBC822-11
100
100
Ectropa|LIMBC821-11
Ectropa|LBEOW2028-11
Ectropa|ANLMN8530-11
26
50
Ectropa|ANLMN8526-11
Ectropa|ANLMN8528-11
Ectropa|ANLMN8527-11
Pseudectropona gen. n.|ANLMN8514-21
93
100
Pseudectropona gen. n.|ANLMN5155-21
Pseudectropona gen. n.|ANLMN8523-21
33
53
Ectropona|LIMBC747-11
99
100
Ectropona|LBEOW2030-11
84
100
Ectropona|LIMBC760-11
Chrysectropa|LBEOW2031-11
100
100
Chrysectropa|LIMBC843-11
Chrysectropa|ANLMN8497-21
Chrysectropa|LIMBC844-11
Chrysectropa|ANLMN8496-21
Chrysectropa|ANLMN8494-21
Chrysectropa|ANLMN8495-21
Chrysectropa|ANLMN8493-21
0.05
Chrysectropa|ANLMN8491-21
Chrysectropa|ANLMN8492-21

Fig. 3. Phylogenetic tree (Maximum-Likelihood, generated by RAxML from complete sequences of 658 bp CO1-5P obtained in BOLD) of 35 specimens from the subfamily Ectropinae s.n. Posterior probabilities and bootstrap values are provided above and below the branches respectively.

morphological differences as discussed below, supports the existence of two distinct genera.

Erythropteryx and three specimens identified as *Chrysopoloma zernyi* recovered as sister to clade E in both analyses but based on morphological components, the recovery of *C. zernyi* here is considered to be an artefact of phylogenetic analyses based solely on COI, as dissection of one of these specimens showed it clearly belongs to *Chrysopoloma*. However, the generic distinction of *Erythropteryx* is supported by the characteristic male genitalia; the general ground-plan is very similar to that of clade E (and hence it can be assumed they are closely related) but *Erythropteryx* has two extremely long, narrow juxta processes whilst in members of clade E these are markedly shorter.

Hamartia s.s. from South Africa recovered as sister to clade E and *Erythropteryx* + *C. zernyi*. The genital morphology of *Hamartia* s.s. from South Africa were found to be distinct, with a very slender, apically rounded gnathos and a long narrow juxta.

The lineage containing *Strigivenifera* was recovered as sister to all other members of clade C, albeit with weak support in the ML analysis (BS = 12) and as a polytomy in the BI analysis. The placement of *Strigivenifera* relative to other genera of the Chrysopolominae is thus unclear, although based on the phylogenetic inferences as well as morphology it certainly belongs within this subfamily and not Ectropinae.

Finally, clade D contained *S. nigrociliata* + *Achrocerides*, which recovered as sister to all other Chrysopolominae. *Scotinocerides nigrociliata* was recovered as sister to *Achrocerides* and although this species shares similarities in external appearance to *Scotinocerides* s.s., these results support distinctions found in the male genitalia that *S. nigrociliata* belongs to a distinct genus. In addition, this species is distributed in West and Central Africa, whilst all other *Scotinocerides* are restricted to southern and eastern Africa.

The two tribes described by Hering (1937), Chrysopolomini and Achroceridini, were not recovered as monophyletic and lacked support from morphological investigations. The character used to distinguish these two tribes, the number of spurs on the hindtibia, has been shown to be homoplastic and not diagnostic at tribal level.

Taxonomic account

Family Chrysopolomidae Aurivillius, 1895
Entomologisk Tidskrift 16: 116–117.

Key to genera

1. Anterior processes of transtilla not medially fused; generally small-sized **2**
– Anterior processes of transtilla medially fused; generally medium-sized **8**
2. Single posterior process of transtilla; distributed on mainland Africa **3**
– Two posterior processes of transtilla completely separated; restricted to Madagascar .... ***Vietteopoloma*** Hering, 1961
3. Ground colour of body and wings white .... ***Chrysopolomides*** Hering, 1937
– Ground colour of body and wings beige, brown, or grey **4**
4. Both fore- and hindwings scalloped, angularly produced at vein M3 .... ***Ectropa*** Wallengren, 1863
– Forewing arcuate; hindwing only scalloped near anal margin **5**
5. Medial line on forewing straight or gently arcuate, pinkish-brown .... ***Chrysectropa*** Bethune-Baker, 1911
– Medial line absent; postmedial line on forewing angled or rounded, black, brown or grey **6**
6. Wings heavily speckled with grey scales; postmedial line on forewing curved, weakly defined and zigzagged .... ***Muscectropa*** gen. n.
– Wings uniform in colour; postmedial line on forewing strongly angled at vein R5 .... **7**
7. Valve with saccular process ***Pseudectropona*** gen. n.
– Valve lacks saccular process .... ***Ectropona*** Kurshakov & Zolotuhin, 2013
8. Venation on wings clearly defined **9**
– No heavy scaling along veins **10**
9. Wing venation strongly defined with brown, larger in size .... ***Strigivenifera*** Hering, 193
– Wing venation finely defined with black, smaller in size ....***Diquishia*** Kurshakov & Zolotuhin, 2016
10. Possesses two pairs of hindtibial spurs **11**
– Possesses one pair of hindtibial spurs **13**
11. Presence of forewing discal spot .... ***Achrocerides*** Hering, 1937
– Absence of forewing discal spot **12**
12. Anterior process of transtilla apically obcordate in shape; distributed in southern or eastern Africa .... ***Scotinocerides*** Hering, 1937
– Anterior process of transtilla apically extremely broad, hammerhead-shaped; distributed in West Africa .... ***Auripoloma*** gen. n.
13. Presence of forewing discal spot, even if weakly defined; wings beige or brown **14**
– Complete absence of forewing discal spot; forewings greyish-pink .... ***Erythropteryx*** Hering, 1937
14. Posterior process of transtilla comprised of two large, medially fused lobes; antennae equal to or less than half the length of forewing .... ***Chrysopoloma*** Bethune-Baker, 1911
– Posterior process of transtilla singular, long, narrow and apically rounded; antennae greater than half the length of forewing; restricted to South Africa .... ***Hamartia*** Hering, 193

Subfamily Ectropinae Hering, 1937
Annals of the Transvaal Museum 17: 236–237.

The subfamily Ectropinae contains mostly small, beige species. In the male genitalia, they possess completely separated anterior processes of the transtilla, a simple juxta and most species also have a narrow valve (with the exception of *Ectropona* species) as well as a longer and larger vesica of the phallus, and are very distinct from the Chrysopolominae. Members of Ectropinae are smaller in size and Hering (1937) also observed that in wing venation, the basal portion of r^{4+5} is mostly absent in Ectropinae but well-developed in Chrysopolominae.

Zolotuhin et al. (2014) transferred the tribe Achroceridini (containing *Strigivenifera* and *Achrocerides*) from Chrysopolominae to Ectropinae, based on reasoning that *Ectropa* possessed "gnathos-like sclerites" in the male genitalia similar to *Strigivenifera* and *Achrocerides*. This is problematic for a number of reasons. Firstly, Zolotuhin et al. (2014) did not include any representatives of Ectropinae in their study believing that *a priori*, it was the "least important" group for their analyses as members of *Strigivenifera* were close in terms of genital morphology; it should be noted that at this point in their review, *Strigivenifera* was still in the subfamily Chrysopolominae. It is also important to consider that all Chrysopolomidae genera possess a gnathos-like transtilla and hence it is probable that Zolotuhin et al. (2014) were referring to the shape of this character being similar in *Ectropa*, *Achrocerides* and *Strigivenifera* and not the presence of the structure itself. If this were the case, the homologous and thus interchangeable use of the terms "gnathos-like sclerites" and "transtilla" in this particular section make it incredibly confusing for the reader and misinterpretations may occur as a result. In order to clarify this issue, the terminology of the genital structures as referred herein are clearly defined and an annotated figure is provided in Fig. 1. The genus *Diquishia* was then described within the tribe Achroceridini in Kurshakov & Zolotuhin (2016), again based on observed similarities with *Strigivenifera* genitalia.

The results of the phylogenetic analyses coupled with further morphological investigations suggest that *Strigivenifera*, *Achrocerides*, and *Diquishia* belong in the Chrysopolominae and are herein transferred back to the subfamily.

Kurshakov & Zolotuhin's (2013a) review of the genus *Ectropa* and description of *Ectropona* provided an excellent contribution to the knowledge of what was previously a monotypic genus, but through further phylogenetic and morphological investigations in this present study, the existence of two further genera has become apparent. Firstly, *Ectropa* was recovered in two clades with very large pairwise distances in the phylogeny as discussed above. One clade comprised the type species of the genus, *E. ancilis* Wallengren, 1863, and *E. alberici* Dufrane, 1945 in the other. Externally, *E. ancilis* has characteristically scalloped hindwings (as also seen in *E. adam* Kurshakov & Zolotuhin, 2013) whilst the hindwings of *E. alberici* are only scalloped at the tornus, similarly to the distinct genus *Ectropona*; the forewings of *E. alberici* are also more rounded than those of *E. ancilis*. *Ectropa alberici* is noticeably larger in size and the wings bear a grey, mottled appearance with only extremely faint postmedial lines compared to the well-defined postmedial lines of *E. ancilis*. In the male genitalia, the clasping apparatus of *E. alberici* is considerably larger, possessing a far narrower and more elongate uncus and a rectangular, plate-like posterior process of the transtilla. The anterior processes of the transtilla of *E. alberici* are considerably longer and more developed than in *E. ancilis*, and the juxta is formed into a shield-like structure compared to the simple juxta of the latter. These morphological characters, coupled with the high divergences found in the DNA barcodes, suggest the existence of a derived member of the subfamily, and thus a new generic name is introduced: *Muscectropa* gen. n.

Ectropona was the only genus to be recovered as paraphyletic within the Ectropinae, a paratype of *E. dargei* Kurshakov & Zolotuhin, 2013, the type species of *Ectropona*, with the BOLD process number LIMBC760-11, clustering separately to three specimens of West African *E. revelli* Kurshakov & Zolotuhin, 2013. Further morphological investigations revealed the male genitalia of *E. dargei* (as well as *E. aarviki* Kurshakov & Zolotuhin, 2013 and *E. kubwe* Kurshakov & Zolotuhin, 2013) to be extremely simplified in comparison to all other Chrysopolomidae, wherein the transtilla lacks apical processes and is comprised of a flat, triangular posterior process and the valve is triangular. The male genitalia of *E. revelli* (and *E. larsa* Kurshakov & Zolotuhin, 2013), however, has a very elongate, pointed posterior process of the transtilla and two short, anterior processes. Perhaps the most distinctive feature to separate *E. revelli* and *E. larsa* from the other three *Ectropona* species is the presence of a saccular process on the valve. Externally, the moths are similar in appearance although the forewing discal spot of *E. revelli* and *E. larsa* is more ovoid or kidney-shaped compared to the rounded discal spot of all other members of *Ectropona*. Whilst Kurshakov & Zolotuhin (2013a) noted the presence of the saccular process in *E. revelli* and *E. larsa* and not in other members of *Ectropona*, the phylogenetic results here strongly suggest these two taxa belong in their own distinct genus; hence, based on the evidence presented above, a new generic name is established for these two species: *Pseudectropona* gen. n.

The placement of the monotypic Madagascan genus *Vietteopoloma* within the Ectropinae is herein maintained. Although not represented in the phylogenetic analyses, *Vietteopoloma* shares several similarities in both the external and genital morphology which support its position within this subfamily. The fore- and hindwing pattern

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and shape is highly reminiscent of *Ectropa*, and the moth is similarly small in size. In the male genitalia, the two posterior processes of the transtilla are completely separated, which is unique within the Ectropinae, although the anterior processes are also separated which is typical of the subfamily. The shape of the phallus is somewhat reminiscent of *Ectropa*, being extremely narrow, strongly sclerotised, and evenly curved whilst the narrow valve which points dorsally at the apex is similar to *Ectropa* and *Chrysectropa*.

The following list comprises the genera and species contained within Ectropinae, with brief genus re-descriptions and diagnoses:

Ectropa Wallengren, 1863
Figs 4, 24
Wiener entomologische Monatschrift 7 (5): 141–142.

Type species. *ancilis* Wallengren, 1863 (by monotypy)

Holotype. ♂.

Type locality. Caffraria orientali [South Africa] (SNHM).

Genus re-description. Small size. Antennae bipectinate, pale beige or golden. Ground colour of head, thorax, abdomen and wings golden-brown or greyish-beige speckled with very small dark brown scales. Forewing broad with scalloped margin angularly produced at vein M3; postmedial line irregularly curved, dark brown or grey; small dark brown or grey discal spot. Distal margin dark brown or dark grey; fringe long, same as ground colour, cilia black in distal quarter. Hindwing scalloped, same colour as forewing, with dark brown or grey postmedial line protruding between veins M2 and Cu1; sometimes with very faint brown discal marking; distal margin dark brown or grey, fringe long, same as ground colour cilia black in distal quarter. Underside. Ground colour and legs golden or greyish-beige; hindtibia with two pairs of spurs. Both wings golden brown or greyish-beige but slightly paler than upperside, postmedial lines of both fore- and hindwings visible; forewing discal spot dark brown, hindwing also with brown discal spot. Male genitalia. Single posterior process of transtilla triangular, rounded apically; paired anterior processes of transtilla narrow, relatively short and completely separated. Valve wide at base and then constricted into a hook, curving dorsally in distal portion. Juxta flat, rectangular. Phallus short, narrow, medially curved.

Diagnosis. *Ectropa* species can be separated from allied taxa based on the scalloped margin of both wings which are strongly produced and angled at vein M3. Within the male genitalia, the combination of the triangular and apically rounded posterior process of the transtilla, the constricted dorsally curved valve and the medially curved phallus are diagnostic for species in this genus.

Distribution. The genus has a disjunct distribution, one species known from South Africa and the other from Tanzania.

Species content
E. ancilis Wallengren, 1863
E. adam Kurshakov & Zolotuhin, 2013

Muscectropa gen. n.
urn:lsid:zoobank.org:act:0F8D69B7-DD29-4920-A6AF-4505C956FECC
Figs 5, 25

Type species. *Ectropa alberici* Dufrane, 1945

Holotype. ♂.

Type locality. Kamituga, DRC (RBINS).

Genus description. Small size. Antennae bipectinate, beige. Ground colour of head, thorax, abdomen and wings pale beige, heavily speckled with small dark grey scales. Forewing broad, rounded, dentate near anal margin; dark grey postmedial line arcuate, ill-defined or incomplete, strongly concave between veins giving it a zig-zagged appearance; discal spot dark grey, rounded or ovoid. Distal margin dark grey, fringe long, same as ground colour, dark grey patch between R2 and R1 of varying size; cilia sometimes dark grey in distal quarter. Hindwing angled just above vein Rs, then scalloped near anal margin; darker grey patch in costal half near distal margin, with faint, zig-zagged postmedial dark grey line; often with rounded, dark grey discal spot. Fringe long, same as ground colour, cilia sometimes black in distal quarter. Underside. Ground colour and legs greyish-beige; hindtibia with two pairs of spurs. Both wings same as upperside, with dark grey postmedial lines and discal spots. Male genitalia. Uncus narrow, elongate, strongly sclerotised apically. Posterior process of transtilla plate-like, rectangular with slight apical depression; anterior processes of transtilla paired, relatively long, narrow. Valve very broad at base then constricted, narrow, and angled dorsally in the distal portion. Juxta very broad, shield-like. Phallus straight, tube-like, with a carinal process ventrally; vesica large, without cornuti but highly scobinate.

Diagnosis. The arcuate, zig-zagged and weakly-defined postmedial band together with the dark grey speckled wings allow the single species of *Muscectropa* to be easily identified. In the male genitalia, the valves are similar to *Ectropa* but in the new genus, the phallus is straight with a carinal process.

Distribution. Distributed throughout the forest belt from Guinea to Nord-Kivu in eastern DRC. Kurshakov & Zolotuhin (2013a) were only aware of specimens from either extreme of its range, however specimens from Cameroon in ANHRT examined as part of this study suggest a continuous distribution.

Etymology. The name of this genus is derived from a combination of the Latin term for moss ('musco') in reference to the mottled, moss-like appearance of the wings of the type species, and the genus *Ectropa* to which it is closely allied.

Species content

M. alberici (Dufrane, 1945)

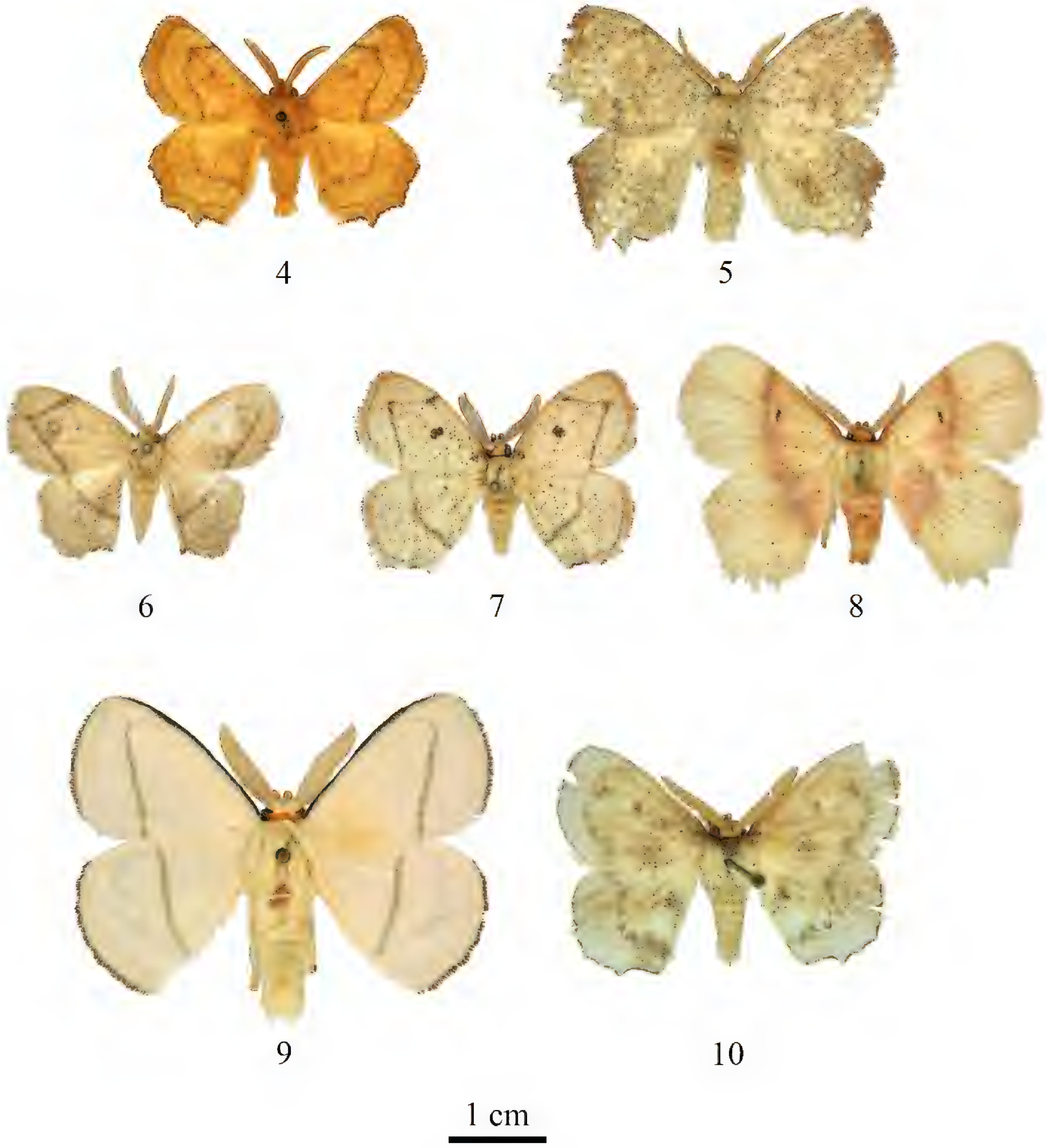
Ectropona Kurshakov & Zolotuhin, 2013
Figs 6, 26
SHILAP Revista de Lepidopterologia 41 (164): 437.

Type species. *Ectropona dargei* Kurshakov & Zolotuhin, 2013 (by original designation)

Holotype. Male.

Type locality. Usambara Mountains, Tanzania (MWW).

Genus re-description. Small size. Antennae bipectinate, beige or pinkish-brown. Ground colour of head, thorax, abdomen and wings beige or pinkish-brown speckled with a few indistinct dark brown scales. Forewing broad, rounded; discal spot rounded. Postmedial line grey to dark brown, sharply angled at vein R5. Distal margin grey or dark brown, fringe long, generally slightly darker than ground colour. Hindwing rounded,



Figs 4–10. Adults. **4**. *Ectropa ancilis*, South Africa (NHMUK). **5**. *Muscectropa alberici*, Ivory Coast (ANHRT). **6**. *Ectropona dargei*, Tanzania (ZSM). **7**. *Pseudectropona revelii*, Liberia (ANHRT). **8**. *Chrysectropa roseofascia*, Ivory Coast (ANHRT). **9**. *Chrysopolomides nivea*, Sierra Leone (ANHRT). **10**. *Vietteopoloma madagascariensis,* Madagascar (MNHN).

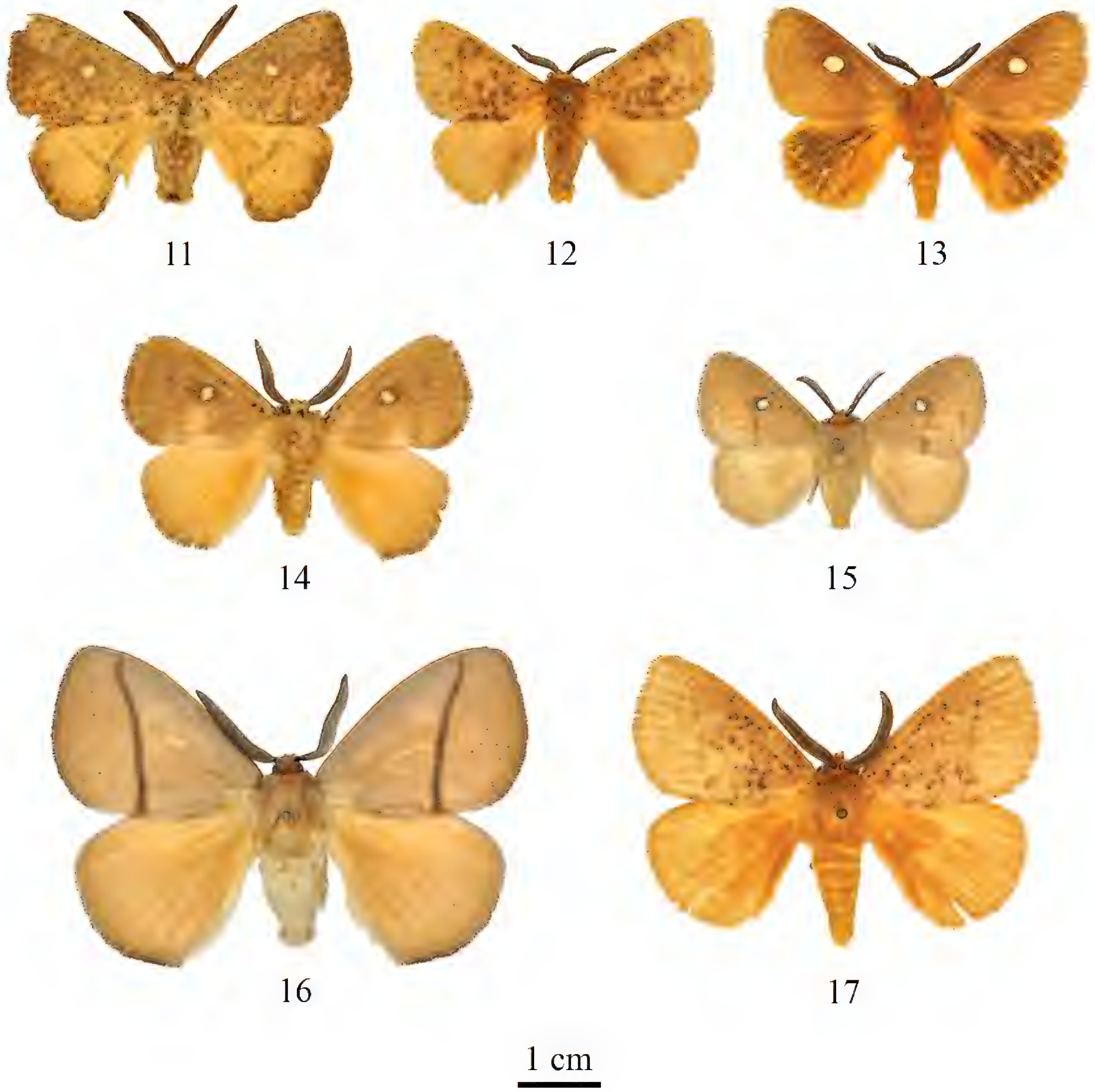
scalloped near anal margin; postmedial line gently arcuate. Fringe long, slightly darker than ground colour, cilia sometimes dark grey in distal quarter. Underside. Ground colour and legs beige or pinkish-brown, hindtibia with two pairs of spurs. Ground colour of wings as upperside, postmedial lines widely convex. Forewing discal spot visible, and discal marking on hindwing also sometimes present. Male genitalia. Single posterior process of transtilla broad triangular; no anterior processes. Valve wide at base, triangular, tapering to a rounded point distally. Phallus very short, with slight curve and large vesica with a single long or group of short cornuti.

Diagnosis. Species of *Ectropona* and *Pseudectropona* both share a very similar habitus with the postmedial line of the forewing sharply angled at vein R5. However, these two sibling genera can easily be separated based on the absence of anterior processes of the transtilla and the broad triangular valves lacking a saccular process in *Ectropona*.

Distribution. Restricted to mountainous regions of eastern Tanzania and south-eastern Kenya.

Species content

E. dargei Kurshakov & Zolotuhin, 2013
E. aarviki Kurshakov & Zolotuhin, 2013
E. kubwe Kurshakov & Zolotuhin, 2013



Figs 11–17. Adults. **11**. *Chrysopoloma rudis*, South Africa (NHMUK). **12**. *Chrysopoloma varia*, Kenya (NHMUK). **13**. *Chrysopoloma bicolor*, South Africa (ANHRT). **14**. *Chrysopoloma zernyi*, Tanzania (ANHRT). **15**. *Chrysopoloma moulini* comb. n., Ethiopia (ZSM). **16**. *Scotinocerides pseudorestricta*, Zambia (ANHRT). **17**. *Scotinocerides fasciata*, Zambia (ANHRT).

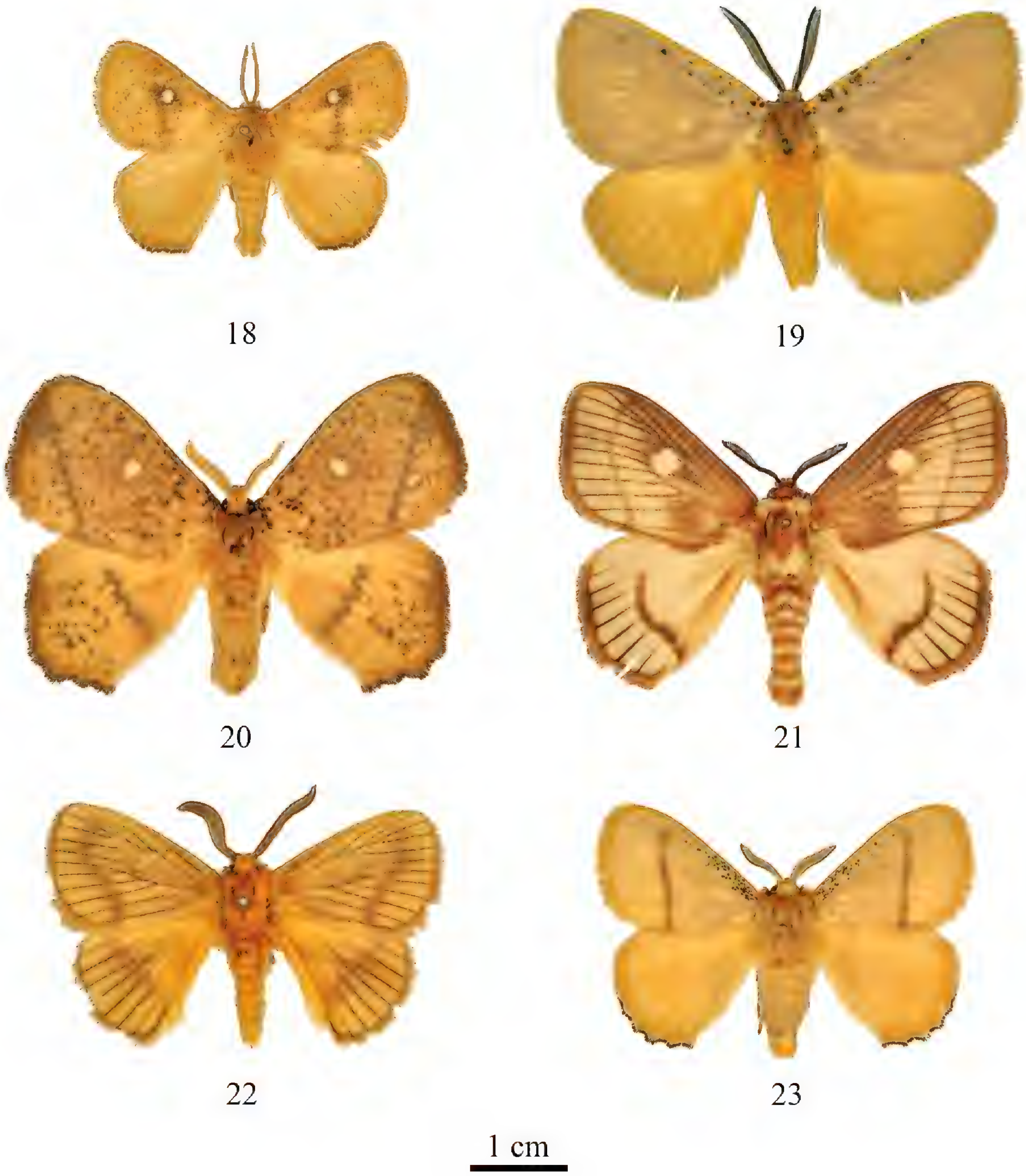
Pseudectropona gen. n.
urn:lsid:zoobank.org:act:3B4A0EEC-8B0F-4A90-873C-DD62C344300F
Figs 7, 27

Type species. *Ectropona revelli* Kurshakov & Zolotuhin, 2013

Holotype. ♂.

Type locality. Bo, Sierra Leone (NHMUK).

Genus description. Small size. Antennae bipectinate, beige. Ground colour of head, thorax, abdomen and wings creamy-beige sparsely speckled with dark brown scales. Forewing broad, rounded; discal spot dark brown, ovoid or reniform. Postmedial line dark brown, sharply angled at vein R5. Distal margin weakly dark brown, fringe long, pale brown, cilia sometimes dark brown in distal quarter. Hindwing rounded, scalloped near anal margin; same colour as forewing with very small, rounded discal spot; postmedial line gently arcuate; fringe as in forewing. Underside. Ground colour and legs beige, hindtibia with two pairs of spurs. Both wings with same ground colour as upperside, postmedial lines widely convex. Forewing discal spot visible, and discal marking on hindwing present. Male genitalia. Uncus broad, rectangular, apically flat with slight medial depression. Posterior process of transtilla triangular, slender, long, apically with a rounded point; anterior processes of transtilla



Figs 18–23. Adults. **18**. *Hamartia medora*, South Africa (NHMUK). **19**. *Erythropteryx roseotincta*, DRC (RMCA). **20**. *Achrocerides theorini*, Liberia (ANHRT). **21**. *Strigivenifera eborea*, Sierra Leone (ANHRT). **22**. *Diquishia ansorgei*, Angola (NHMUK). **23**. *Auripoloma nigrociliata* comb. n., Togo (ANHRT).

paired, short, rounded. Valve tapered, apically rounded, with narrow saccular process on anal margin, setose apically. Juxta broad, short, rounded. Phallus tube-like, curved in proximal third; vesica large, membranous, with cluster of dense, short cornuti.

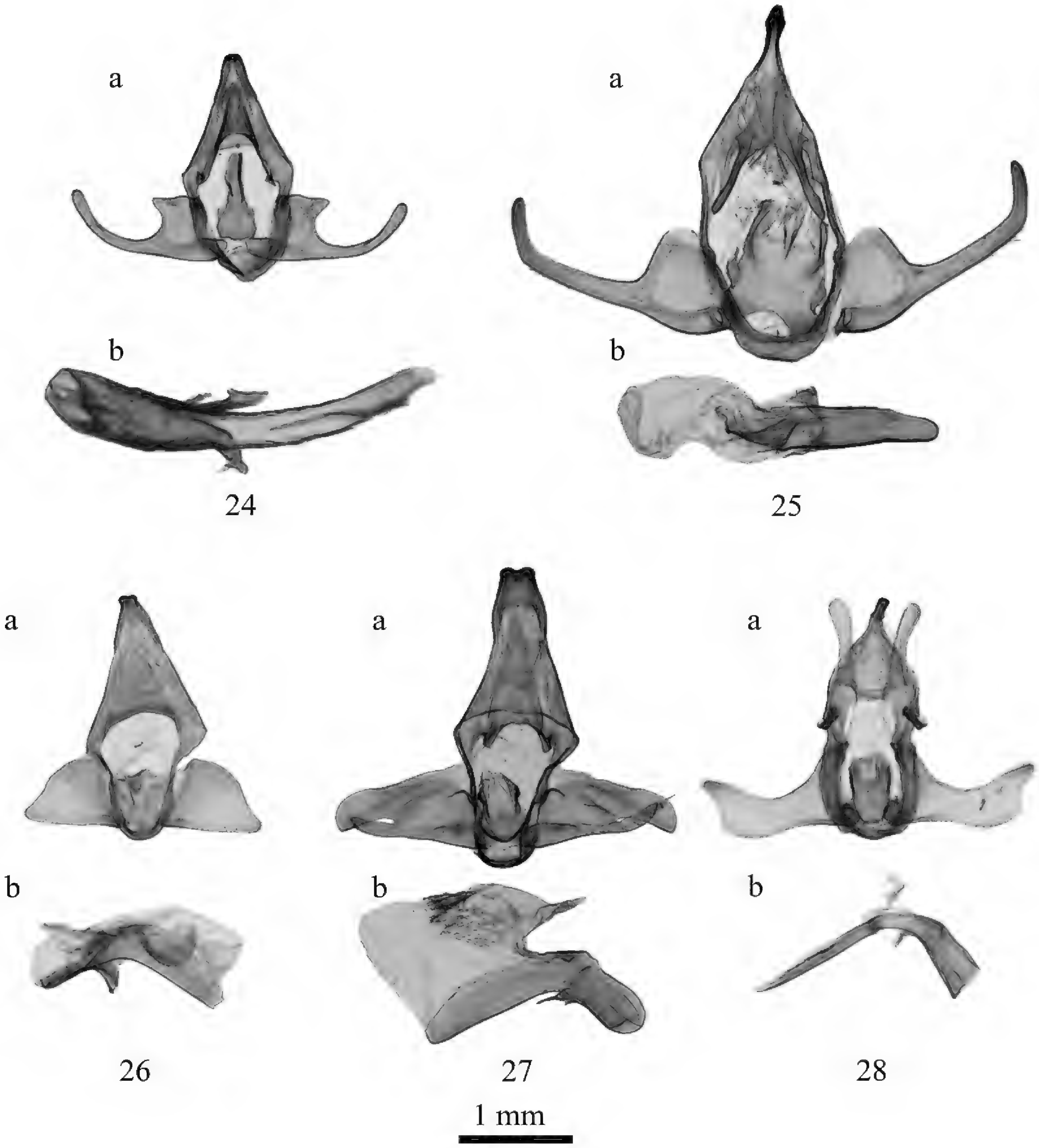
Diagnosis. As discussed under the very similar *Ectropona* above, *Pseudectropona* species can only be readily identified from the genitalia. In the new genus, the presence of the anterior process of the transtilla and the saccular process of the valve, a synapomorphy of this genus, together with the curved phallus allow for easy identification. Although based on a limited number of specimens, it is possible that the two genera are allopatrically distributed across the Great Rift Valley, *Ectropona* to the east and *Pseudectropona* to the west.

Distribution. Both species in this genus are forest insects although they appear to have a disjunct distribution, the type species found in the Upper Guinean Forests and the other in the easternmost extent of the Congo Basin forests.

Etymology. The new genus name is in reference to the similarities with its sibling genus *Ectropona*.

Species content

P. revelli (Kurshakov & Zolotuhin, 2013)
P. larsa (Kurshakov & Zolotuhin, 2013)



Figs 24–28. Male genitalia (a = clasping apparatus; b = phallus). **24**. *Ectropa ancilis*, South Africa, genitalia slide No. TT 216 (ANHRT). **25**. *Muscectropa alberici*, Ivory Coast, genitalia slide No. TT 214 (ANHRT). **26**. *Ectropona dargei*, Tanzania, genitalia slide No. ZSM Sp. 1596 (ZSM). **27**. *Pseudectropona revelli*, Liberia, genitalia slide No. TT 213 (ANHRT). **28**. *Vietteopoloma madagascariensis*, Madagascar, genitalia slide No. TT 218 (MNHN).

Chrysectropa Bethune-Baker, 1911
Figs 8, 29
Annals & Magazine of Natural History (8) 7 (42): 566–567.

Type species. *Chrysopoloma roseofascia* Aurivillius, 1900 (by original designation)

Syntypes. 1 ♂, 1 ♀.

Type locality. N'Dalla Tando, Angola (NHMUK).

Genus re-description. Small size. Antennae bipectinate, beige. Head, thorax and abdomen yellow-beige. Forewing broad, rounded, creamy beige, sometimes slightly golden, slightly darker patch approximately between veins R4 and M2; sprinkled sparsely with a few tiny black scales. Discal spot extremely small, comprised of a cluster of black scales. Medial line broadened, pinkish-brown, diffuse, very slightly arcuate. Fringe long, same as ground colour. Hindwing rounded, gently scalloped near anal margin, same colour as forewing accentuated with additional tiny black scales. Antemedial line pinkish-brown, diffused, gently arcuate; fringe as in forewing. Underside. Ground colour and legs yellow-beige, hindtibia with two pairs of spurs. Both wings with same ground colour as upperside, sprinkled with tiny black scales; both fore- and hindwing with small oblong black discal spot. Forewing medial line and hindwing antemedial line as on upperside. Male genitalia. Single posterior process of transtilla fairly short, rectangular, with very slight apical depression; paired anterior processes of transtilla extremely short, rounded, completely separated. Valve wide at base, tapered, narrow, curved distally. Juxta broad, flat, with narrow, rounded central process. Phallus short, large vesica with rounded plate of dense, short cornuti.

Diagnosis. The single known species of *Chrysectropa* has a distinctive appearance, with no other Chrysopolomidae displaying a broadened medial band that is pinkish-brown in colour.

Distribution. Widely distributed in West and Central Africa.

Species content

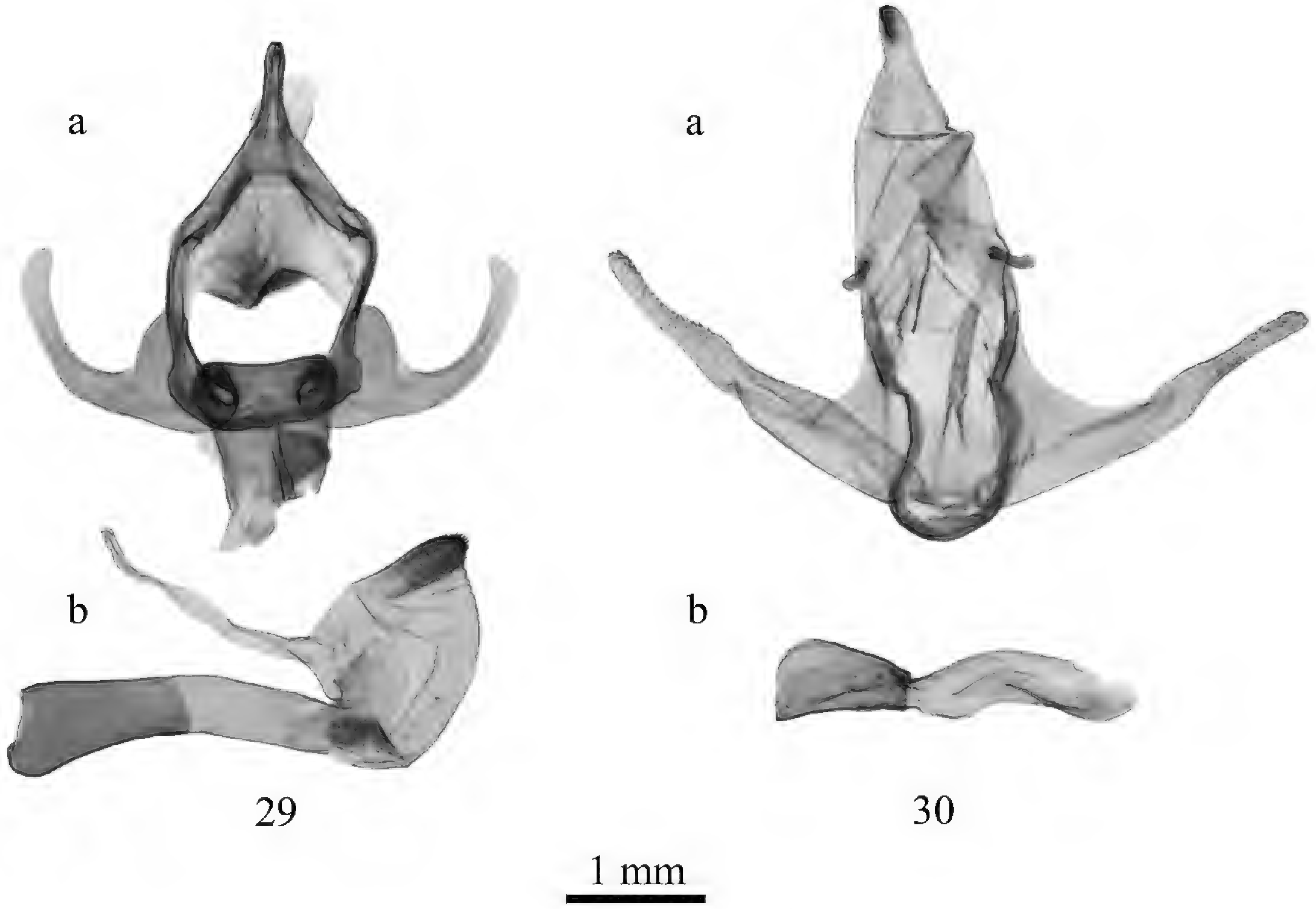
C. roseofascia (Aurivillius, 1900)
= *C. unilinea* Bethune-Baker, 1911

Chrysopolomides Hering, 1937
Figs 9, 30
Annals of the Transvaal Museum 17: 240.

Type species. *Chrysopoloma nivea* Aurivillius, 1903 (by original designation)

Holotype. ♂.

Type locality. Bipindi, Cameroon (MfN).



Figs 29–30. Male genitalia (a = clasping apparatus; b = phallus). **29**. *Chrysectropa roseofascia*, Gabon, genitalia slide No. TT 179 (ANHRT). **30**. *Chrysopolomides nivea*, Liberia, genitalia slide No. TT 107 (ANHRT).

Genus re-description. Medium size. Antennae bipectinate, white, flagellum beige. Ground colour of head, thorax, abdomen and wings white; collar and palps orange. Forewing broad, outer margin arcuate; costal margin black; postmedial line dark brown, straight, gently kinked between veins R2 and R3. Fringe long, pale cream, cilia dark brown in distal quarter. Hindwing rounded, medial line dark brown, generally straight but with very slight undulation; fringe as in forewing. Underside. Ground colour as upperside, legs orange, hindtibia with one pair of spurs. Forewing with brown, gently undulating postmedial line and dark brown, crescent-shaped discal dash. Hindwing with brown postmedial line, kinked between veins M2 and M3 and small, rounded brown discal spot. Male genitalia. Single posterior process of transtilla relatively short, narrow, rounded; paired anterior processes of transtilla short, bulb-shaped, completely separated. Valve wide at base, tapered, narrow, long, rounded distally, finely scobinate in distal half. Juxta broad at base, with long, narrow, distally rounded central process. Phallus short.

Diagnosis. The single species of *Chrysopolomoides* is unmistakable with no other Chrysopolomidae exhibiting a pearlescent white ground-colour of the wings and body.

Distribution. Widespread in forested regions of West and Central Africa.

Species content

C. nivea (Aurivillius, 1903)

Vietteopoloma Hering, 1961

Figs 10, 28

Bulletin de la Société entomologique de France 65 (9–10): 303.

Type species. *Vietteopoloma madagascariensis* Hering, 1961 (by original designation)

Holotype. ♂.

Type locality. Ambatovositra, Madagascar (MNHN).

Genus re-description. Small size. Antennae bipectinate, beige. Head and palps beige, collar dark brown, thorax and abdomen pale cream speckled with black spots. Forewing broad, rounded, gently scalloped, pale brown near thorax but creamy beige beyond postmedial line, speckled with black spots in proximal half near anal margin, margins dark brown; postmedial line dark brown, arcuate, crenulate, displaced between vein R4 and M1; discal spot diffuse, small, rounded, dark brown; fringe long, beige. Hindwing rounded, gently scalloped, slightly paler than forewing; medial line dark brown, undulate; discal spot small, black, surrounded by black speckling; fringe long, beige. Underside. Ground colour and legs pale beige, hindtibia with two pairs of spurs. Both wings creamy beige, with undulate, brown postmedial lines. Discal spot of both wings small, rounded, brown. Male genitalia. Paired posterior processes of transtilla completely separated, long, narrow, and bulb-shaped apically; paired anterior processes of transtilla short, thin, rounded, and completely separated. Valve moderately wide, pointed dorsally at apex. Juxta short, shield-like. Phallus long, extremely narrow, bent medially.

Diagnosis. *Vietteopoloma madagascariensis* is phenotypically reminiscent of *Muscectropa* species in terms of the rounded postmedial line of the forewing and has affinities with *Ectropa* species based on the shape of the phallus, but the separated posterior processes of the transtilla is a synapomorphy of this genus.

Distribution. Endemic to Madagascar where it is rare; only three specimens, all in MNHN, have been examined as part of this study.

Species content

V. madagascariensis Hering, 1961

Subfamily Chrysopolominae Hering, 1937

Annals of the Transvaal Museum 17: 237–238.

The subfamily Chrysopolominae consists of medium-sized brown or beige moths with broad, rounded wings and bipectinate antennae. In the male genitalia, the most typical feature is the medially fused anterior processes of the transtilla but they also all possess a well-developed juxta.

The two tribes described by Hering (1937), Chrysopolomini and Achroceridini, were not recovered as monophyletic in the DNA analyses and lacked support from morphological investigations. This is unsurprising considering these two tribes were erected based on the numbers of spurs of the hindtibia, Hering (1937) having clearly provided a caveat that this character was "irrelevant for phyletic inferences" and that the tribal divisions were more for "convenience". It has been shown that this character is homoplastic and although not diagnostic at the tribal level, it nevertheless holds true at the generic level throughout Chrysopolomidae. Zolotuhin et al. (2014) however maintained the tribal system based on the similarities of wing pattern, number of tibial spurs and the structure of the transtilla without critically investigating the rather arbitrary nature of Hering's tribes, while Kurshakov & Zolotuhin (2016) used a similar argument to place *Diquisha* within Achroceridini focusing on genital similarities rather than the "spur formula" which was not in keeping with other members of the tribe.

It is possible that from a cursive look, *Strigivenifera* and *Achrocerides* could be placed within the same tribe due to similarities in the male genitalia but these genera did not cluster together in the phylogenetic analyses. Furthermore, it could be surmised that *Diquishia* would be more suited to the tribe Chrysopolomini as opposed to Achroceridini based on distinctions in the external morphology. With the alternative being to erect numerous new tribes, it is concluded herein that Hering's tribal system is unreliable and is thus dismissed.

In the results of the phylogenetic analyses, clade E consisted of *Chrysopoloma* and *Scotinocerides* s.s. In the male genitalia, members of both clusters share many affinities, namely a transtilla with two large, medially fused posterior lobes and two large, medially fused, square or rounded anterior lobes, as well as a juxta comprised of a central process with two lateral processes and a near-identical phallus. A distinction was identified however, whereby the uncus of *Scotinocerides* is noticeably longer and pointier than in the related genus. Externally, all members of clade E are recognisably similar, with broad, rounded, beige wings, although members of *Scotinocerides* are larger and typically possess a postmedial forewing line whilst *Chrysopoloma* display a rounded discal spot. An additional distinctive feature between the two genera can be seen in the number of hindtibia spurs, wherein *Scotinocerides* possesses two pairs whilst *Chrysopoloma*, and indeed all other members of clade C only have one pair. As such, based on the aforementioned evidence, *Scotinocerides* and *Chrysopoloma* are maintained as distinct genera. One taxon, *Chrysopoloma restricta* Distant, 1899 possesses all of the characteristics of *Scotinocerides* and is thus transferred into this genus: *Scotinocerides restricta* (Distant, 1899) comb. n.

The recovery of species of *Hamartia* from Ethiopia within *Chrysopoloma* s.l. in the phylogenetic analyses was considered surprising at first. Despite externally being very similar to *Chrysopoloma* species, these are typically slightly smaller, with a smaller, more defined discal spot and can thus be readily distinguished. However, the male genitalia of these *Hamartia* specimens were found to be identical in structure to *Chrysopoloma*. *Hamartia medora moulini* Rougeot, 1977 is hence raised to species level, and transferred to *Chrysopoloma* thus: *Chrysopoloma moulini* (Rougeot, 1977) comb. n. The taxon *Hamartia paupera johanni* Rougeot, 1977 was described in *Hamartia* despite its nominotypical subspecies having been described as a *Chrysopoloma*; it is hence assumed that Rougeot (1977) implicitly transferred *C. paupera* Hering, 1925 to *Hamartia*. Both *H. p. paupera* and *H. p. johanni* are thus transferred to *Chrysopoloma*: *Chrysopoloma paupera paupera* Hering, 1925 stat. rev., *Chrysopoloma paupera johanni* (Rougeot, 1977) comb. n.

The remaining *Hamartia* species, *H. medora* Hering, 1937 and *H. clarissa* Hering, 1937, were found in both genetic and morphological analyses to be distinct from other *Chrysopoloma*. It is likely that this genus, containing species distributed in southern and eastern South Africa are only found in these regions which exhibit unique fynbos and upland habitats that are home to many endemic taxa.

Scotinocerides nigrociliata was recovered in the DNA analyses as sister to *Achrocerides*. Although this species is close in appearance to *Scotinocerides*, it can be distinguished by the following characters: it is noticeably smaller and more compact than other *Scotinocerides* that possess a postmedial line on the forewing whilst in the male genitalia it possesses a very large, broad transtilla, the valve is much wider at the base and the gnathos lobes are narrower and not fused apically. Based on the position of this taxon in the phylogeny and the markedly different male genitalia, a new genus is founded thus: *Auripoloma* gen. n.

Strigivenifera and *Achrocerides* were recovered in the Chrysopolominae and are quite distinct from the Ectropinae (*contra* Zolotuhin et al. (2014)). In the male genitalia, they possess medially fused anterior processes of the transtilla typical of the Chrysopolominae, whilst the juxta is comprised of two caudal processes. Although *Diquishia* was not included in the phylogenetic analyses, the external morphology (especially that of *D. ansorgei* (Bethune-Baker, 1911) is much more reminiscent of Chrysopolominae than other members of the Ectropinae. For instance, *D. ansorgei* is considerably larger in size than all members of Ectropinae and it also possesses a faint discal spot on the forewing as seen in the vast majority of Chrysopolominae species. In the male genitalia, the anterior processes of the transtilla are medially fused and not separated as in the Ectropinae. However, it is likely that *Diquishia* is a derived genus within Chrysopolominae possessing finely marked black veins on the wings, as well as a uniquely shaped phallus which is extremely broad in the anterior half but strongly constricted medially (both synapomorphies of this genus). In addition, both species of the genus appear to be endemic to Angola.

The following list comprises the genera and species contained within Chrysopolominae, with brief genus re-descriptions and diagnoses:

Chrysopoloma Druce, 1886

Figs 11–15, 31–34
Proceedings of the Zoological Society of London 1886: 410.

Type species. *Lasiocampa rudis* Walker, 1865 (by subsequent designation (Aurivillius, 1895: 118))

Syntypes. 2 ♂♂.

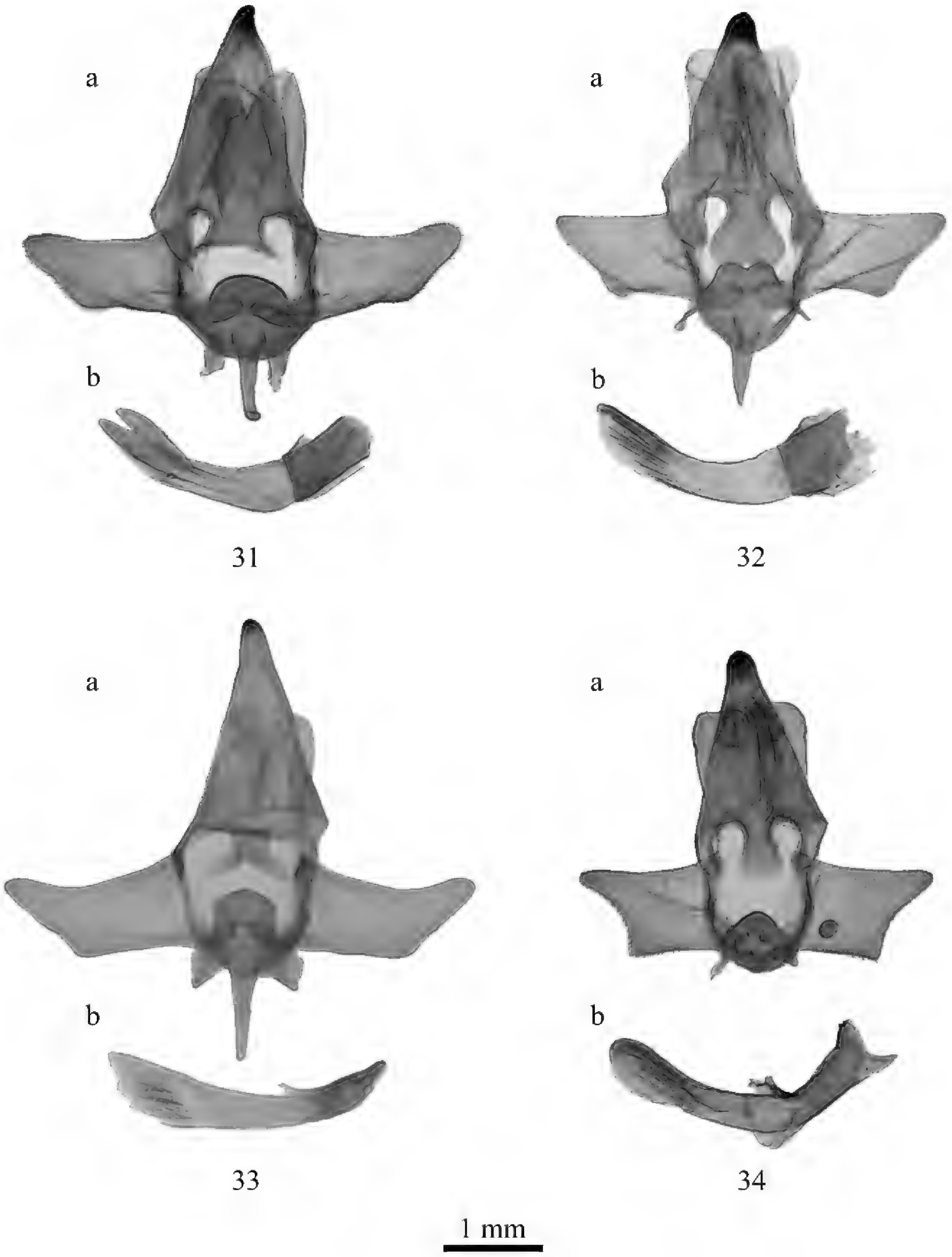
Type locality. Natal, South Africa (NHMUK).

Genus re-description. Medium size. Antennae bipectinate, dark grey to black, flagellum dark beige or black. Ground colour of body and wings uniform pale cream to tawny brown with varying levels of brown or black speckling. Forewing broad with arcuate outer margin; discal spot pale with dark margin, well-defined in most species; indistinct postmedial band in some species. Fringe long, darker than ground colour, occasionally with black interveinal crenulations. Hindwing mostly without markings but may display dark basal sections. Underside. Ground colour similar to upperside but with fewer markings; forewing discal spot often showing through. Legs beige or light orange, sometimes with brown speckling.

Hindtibia with one pair of spurs. Male genitalia. Uncus triangular, apically rounded, paired posterior processes of transtilla closely fused medially, creating a rounded or truncate lobe-like structure with a medial depression. Single, central anterior process of transtilla broad, generally obcordate, varying in length. Valve wide, sometimes slightly medially constricted, with slight concavity on distal edge. Juxta with two pointed lateral processes and longer central process. Phallus moderate length, distally ridged, membranous, with slight medial split; vesica relatively short, membranous.

Diagnosis. Species of *Chrysopoloma* and *Scotinocerides* are very similar in appearance but members of the former are smaller and typically possess a rounded discal spot on the forewing which is absent in the latter. The two genera however can easily be distinguished based on the number of tibial spurs, *Chrysopoloma* with one pair and *Scotinocerides* with two. In the male genitalia, the uncus is triangular, apically rounded and noticeably shorter in *Chrysopoloma* compared to its sibling genus.

Distribution. *Chrysopoloma* species are associated with woodland and forest-savanna mosaic habitats, the majority of species being found in southern and eastern Africa as far north as Ethiopia, with a few species known from further west in Cameroon and Ivory Coast.



Figs 31–34. Male genitalia (a = clasping apparatus; b = phallus). **31**. *Chrysopoloma rudis*, South Africa, genitalia slide No. NHMUK 010317731 (NHMUK). **32**. *Chrysopoloma isabelline*, Zambia, genitalia slide No. TT 182 (ANHRT). **33**. *Chrysopoloma zernyi*, Tanzania, genitalia slide No. TT 192 (ANHRT). **34**. *Chrysopoloma moulini* comb. n., Ethiopia, genitalia slide No. NHMUK 010317735 (NHMUK).

Species content

C. rudis (Walker, 1865)
C. bicolor (Distant, 1897)
C. conspersa (Kirby, 1896)
C. crawshayi Aurivillius, 1904
C. isabellina Aurivillius, 1895
C. moulini (Rougeot, 1977) comb. n.
C. occidens Basquin, 2016
C. pallens Hering, 1925
C. paupera paupera Hering, 1925 stat. rev.
C. paupera johanni (Rougeot, 1977) comb. n.
C. similis Aurivillius, 1895
C. varia varia Distant, 1899
C. varia flavipennis Hering, 1937
C. varia flaviceps Aurivillius, 1901
C. variegata variegata Hering, 1937
C. variegata nigromaculata Hering, 1937
C. zernyi Hering, 1941

Scotinocerides Hering, 1937

Figs 16–17, 35–36
Annals of the Transvaal Museum 17: 241.

Type species. *Chrysopoloma conspurcata* Aurivillius, 1895 (by original designation)

Holotype. ♂.

Type locality. Lindi, Deutsch-OstAfrika [Tanzania] (MfN).

Genus re-description. Medium to large size. Antennae bipectinate, dark grey to black, flagellum dark beige or black. Ground colour of body and wings beige to light brown with varying levels of brown or black speckling. Forewing broad with arcuate outer margin; postmedial line well-defined in most species, light or dark brown, straight or gently concave, sometimes kinked at vein R2. Fringe long, slightly darker than ground colour. Hindwing without markings, generally more yellow in colour than forewing. Underside. Ground colour similar to upperside but with fewer markings; postmedial line often showing through. Legs beige or light orange, sometimes with brown speckling. Hindtibia with two pairs of spurs. Male genitalia. Uncus elongate, pointed apically, paired posterior processes of transtilla fused medially, forming a rounded lobe-like structure with a deep central separation. Single, central anterior process of transtilla broad, generally obcordate, varying in length. Valve wide, sometimes medially constricted, with concavity on distal edge. Juxta with two pointed lateral processes and longer central process. Phallus moderate length, distally ridged, membranous, with slight medial split; vesica relatively short, membranous.

Diagnosis. As discussed under the diagnosis section of *Chrysopoloma*, these two genera are very similar. *Scotinocerides* species are in general a larger insect, possess two pairs of tibial spurs and in the male genitalia, the uncus is elongate and pointed apically.

Distribution. Distributed throughout southern and eastern Africa.

Species content

S. conspurcata conspurcata Aurivillius, 1895
S. conspurcata varioides Hering, 1937
S. fasciata Hering, 1937
S. microsticta Bethune-Baker, 1911
S. pseudorestricta pseudorestricta Hering, 1937
S. pseudorestricta flavina Hering, 1937
S. restricta (Distant, 1899) comb. n.
S. sigma Hering, 1937

Hamartia Hering, 1937

Figs 18, 37
Annals of the Transvaal Museum 17: 248–249.

Type species. *Hamartia medora* Hering, 1937 (by original designation)

Holotype. ♂.

Type locality. Marieps Mountain, South Africa (TMSA).

Genus re-description. Medium size. Antennae bipectinate, beige. Ground colour of head, thorax, abdomen and wings beige speckled with small dark brown scales. Forewing broad, rounded; discal spot white, rounded, outlined in dark brown; medial line dark brown, diffuse often present only from discal spot to anal margin but sometimes completely absent. Fringe long, slightly darker than ground colour. Hindwing without makings; fringe as in forewing but cilia sometimes black in distal portion. Underside. Ground colour beige; hindtibia with one pair of spurs. Fore- and hindwings beige generally without markings; hindwing speckled with brown scale spots. Male genitalia. Single posterior process of transtilla long, narrow, apically rounded; single, central anterior process moderately broad, obcordate. Valve wide, tapered distally to rounded point on costal edge. Juxta rectangular, apically with two short, lateral triangular projections. Phallus moderately long, distally slightly ridged, membranous, with slight medial split; vesica relatively short, membranous.

Diagnosis. In size and general appearance, most noticeably the forewing discal spot, the two *Hamartia* species could be confused with some *Chrysopoloma* species; however, the genital morphology is very distinctive, with a very slender, apically rounded gnathos and a long narrow juxta.

Distribution. Restricted to South Africa.

Species content

H. medora Hering, 1937
H. clarissa Hering, 1937

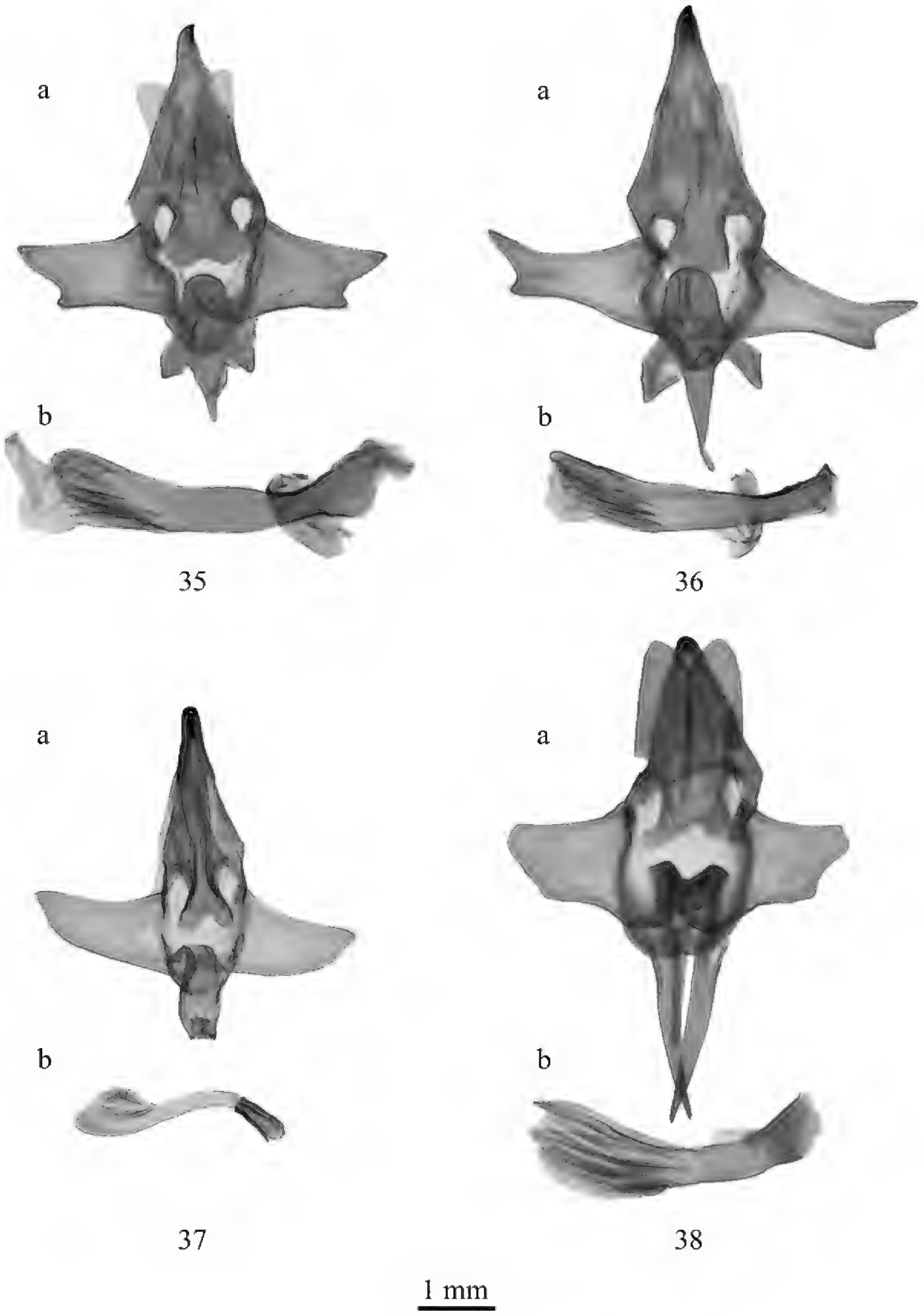
Erythropteryx Hering, 1937
Figs 19, 38
Annals of the Transvaal Museum 17: 247–248.

Type species. *Erythropteryx roseotincta* Hering, 1937 (by original designation)

Holotype. ♂.

Type locality. Elisabethville [Lubumbashi], DRC (RMCA).

Genus re-description. Medium size. Antennae long, black, bipectinate. Head and thorax greyish-pink, abdomen orange. Forewing broad, greyish-pink or beige, speckled with black scales along costal margin. Costal margin orange. Fringe long, same as ground colour; cilia sometimes orange in distal half. Hindwing orange, sometimes tinged with greyish-pink in distal half; fringe as in forewing. Underside. Ground colour uniformly beige or greyish-beige; hindtibia with one pair of spurs; hindwing with black scale spots along costal margin. Male genitalia. Paired posterior processes of transtilla closely fused medially, creating a lobe-like structure with a small medial depression. Single, central anterior process of transtilla broad, obcordate. Valve wide, short, rounded distally and slightly concave. Juxta with two very long, narrow, apically pointed lateral processes and slightly shorter, narrow, apically rounded central process. Phallus moderate length, ridged in distal half, membranous, with slight medial split; vesica short, membranous.



Figs 35–38. Male genitalia (a = clasping apparatus; b = phallus). **35**. *Scotinocerides pseudorestricta*, South Africa, genitalia slide No. TT 184 (ANHRT). **36**. *Scotinocerides fasciata*, Tanzania, genitalia slide No. ZSM Sp. 1597 (ZSM). **37**. *Hamartia medora*, South Africa, genitalia slide No. TT 190 (ANHRT). **38**. *Erythropteryx roseotincta*, DRC, genitalia slide No. TT 205 (RMCA).

Diagnosis. *Erythropteryx* shares affinities with its sister genera *Chrysopoloma* and *Scotinocerides* in terms of its habitus, but the forewing is uniform aside from dark speckling along the costa and it appears to always lack the forewing discal spot, often present in the former and the forewing postmedial line which is a characteristic of the latter. The juxta in the male genitalia of *E. roseotincta* is however very characteristic with two very long lateral processes, which are considerably shorter in members of the aforementioned two genera.

Distribution. The single species in this genus is currently known only from the type locality in Haut-Katanga, DRC. It will almost certainly be present in Zambia but despite reasonably extensive sampling in the Copperbelt, it has not yet been found.

Species content

E. roseotincta Hering, 1937

Achrocerides Hering, 1937
Figs 20, 39
Annals of the Transvaal Museum 17: 241.

Type species. *Chrysopoloma theorini* Aurivillius, 1891 (by original designation)

Syntypes. 2 ♂♂.

Type locality. Gabon [Gabon Estuary at Libreville, Gabon] (SNHM, MfN).

Genus re-description. Medium size. Ground colour beige to tawny-brown, sparsely speckled with black scale spots. Antennae bipectinate, ochreous yellow. Forewing rounded, with pale rounded discal spot; grey postmedial line kinked near outer margin at vein M1; diffuse grey-brown triangular patch on outer margin between veins R3 and M1; hindwing rounded with dentate margin at tornus, grey medial line, speckled with black scale spots in distal half; often with pale, diffuse grey-brown triangular patch on outer margin between veins M1 and M2. Underside. Ground colour of body and wings uniformly pale beige; legs darker and slightly golden; hindtibia with one pair of spurs. Fore- and hindwing with irregular grey scale spots concentrated mostly along the costal margin. Forewing discal spot visible through wing. Diffuse pale grey-brown triangular patch on outer margin between veins R3 and M1 on forewing and between veins M1 and M2 on hindwing. Male genitalia. Paired posterior processes of transtilla long, narrow, pointed apically, fused medially with a membrane; paired anterior processes narrow, moderately long, fused medially with a membrane. Valve wide, truncate, or triangular with distally rounded point. Juxta strongly sclerotised and rounded at base, with two long, apically pointed lateral processes. Phallus relatively long, ridged distally, membranous, with slight medial split; vesica very short, membranous.

Diagnosis. It is possible that members of the genus *Achrocerides* might be confused with *Strigivenifera* species based on their size and the pale forewing discal spot but can easily be distinguished by the lack of fine contrasting scaling along the veins and the presence of blackish-grey speckles on both wings, as well as the dentate margin of the hindwing tornus. In addition, *Achrocerides* species have two pairs of hindtibial spurs whilst only one pair is present in *Strigivenifera* species.

Distribution. Widely distributed in the forested regions of West and Central Africa.

Species content

A. theorini (Aurivillius, 1891)
A. flavoantennata (Berio, 1937)
A. smithi Taberer & Giusti, in prep

Strigivenifera Hering, 1937
Figs 21, 40
Annals of the Transvaal Museum 17: 247

Type species. *Chrysopoloma venata* Aurivillius, 1895 (by original designation)

Holotype. ♂.

Type locality. Lambaréné, Gabon (MfN).

Genus re-description. Medium size. Antennae bipectinate, black. Head ochreous orange, thorax beige with central ochreous orange patch, and abdomen banded with beige and ochreous orange. Forewing broad with rounded apex, ground colour beige, basal half strongly diffused with brown scales; sometimes with brown triangular patch between veins R4 and M2; veins strongly highlighted in brown along their entire length; discal spot pale beige; postmedial band pale brown, kinked at vein M1; fringe long, brown. Hindwing ground colour identical to forewing, veins strongly highlighted in brown beyond the postmedial band. Postmedial band broader than that of forewing, either straight or arcuate; fringe long, brown. Underside. Uniformly beige, legs ochreous orange; hindtibia with one pair of spurs. Male genitalia. Posterior process of transtilla medially split into two relatively narrow, apically rounded processes; anterior processes of transtilla medially fused, narrow, with two thin apically rounded proximo-lateral processes. Valve generally wide, tapered. Juxta strongly sclerotised and rounded at base, with two moderately long, apically pointed lateral processes. Phallus relatively long, membranous distally, sometimes with cornuti-like structures distally.

Diagnosis. *Strigivenifera* species are striking insects, easily distinguished based on the combination of fine brown venation of the wings and a pale forewing discal spot. The only other genus that displays similar venation is *Diquisha*, but the veins are highlighted with black scales, the moths are noticeably smaller and the juxta consists of only a single apically pointed central process.

Distribution. Species of this genus are widely distributed throughout the forests and forest-savanna mosaics of West and Central Africa extending as far south as northern Zambia.

Species content

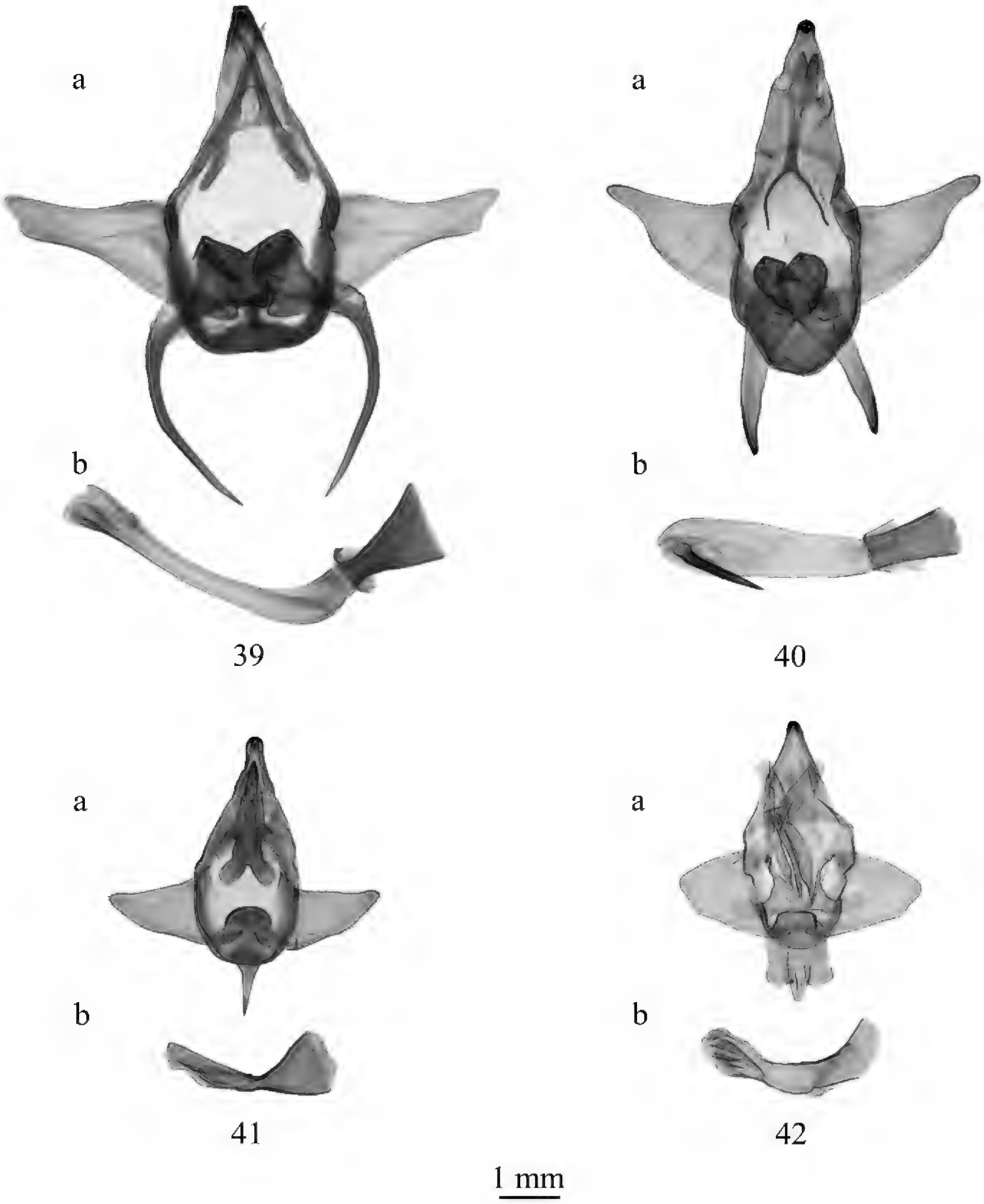
- *S. venata* (Aurivillius, 1895)
- *S. albidiscalis* (Hampson, 1910)
  - = *S. cruisa* Kurshakov & Zolotuhin, 2013
  - = *S. livingstonei* Kurshakov & Zolotuhin, 2013
- *S. bartschi* Kurshakov & Zolotuhin, 2013
  - = *S. tatooifera* Kurshakov & Zolotuhin, 2013
- *S. eborea* Kurshakov & Zolotuhin, 2013
  - = *S. ocellaris* Kurshakov & Zolotuhin, 2013
- *S. marina* Kurshakov & Zolotuhin, 2013
- *S. neo* Kurshakov & Zolotuhin, 2013
- *S. oris* Kurshakov & Zolotuhin, 2013
- *S. smithi* Taberer, 2022
- *S. tanja* Kurshakov & Zolotuhin, 2013

Diquishia Kurshakov & Zolotuhin, 2016
Figs 22, 41
Entomofauna Zeitschrift für Entomologie 37 (2): 33–40.

Type species. *Diquishia morion* Kurshakov & Zolotuhin, 2016 (by original designation)
Holotype. ♂.

Type locality. N slopes of Mt. Hole, Angola (MWW).

Genus re-description (the unique holotype of the type species could not be examined and the re-description is based on the original description as well as through examination of the congeneric *D. ansorgei*). Medium size. Ground colour of head, abdomen, thorax, wings and fringe dark grey or golden-yellow. Forewing broad, outer margin arcuate; veins highlighted with fine black scaling;



Figs 39–42. Male genitalia (a = clasping apparatus; b = phallus). **39**. *Achrocerides theorini*, Gabon, genitalia slide No. TT 131 (ANHRT). **40**. *Strigivenifera venata*, Gabon, genitalia slide No. TT 119 (ANHRT). **41**. *Diquishia ansorgei*, Angola, genitalia slide No. NHMUK 010317733 (NHMUK). **42**. *Auriopoloma nigrociliata*, Togo, genitalia slide No. TT 187 (ANHRT).

sometimes with faint discal spot and curved postmedial band. Hindwing with evenly arcuate margin, veins highlighted with fine black scaling disappearing weaker in the basal section; sometimes with arcuate, postmedial band. Underside. Ground colour as upperside. Veins highlighted with light brown scales. Hindtibia with one or two pair of spurs (see diagnosis below). Male genitalia. Single posterior process of transtilla relatively narrow, apically rounded; single, central anterior process of transtilla moderately broad, obcordate. Valve wide, tapered. Juxta rounded at base, with slender, apically pointed central process. Phallus relatively short, anteriorly very wide and then medially constricted.

Diagnosis. The type species of *Diquisha* and *D. ansorgei*, which was placed in the same genus based on similar external morphology by Kurshakov & Zolotuhin (2016) are distinctive species, displaying fine black venation on both wings. Kurshakov & Zolotuhin (2016) were unable to study the male genitalia of *D. ansorgei* but upon dissection of several specimens as part of this current study, it appears these two species are congeneric based on the ground-plans, especially the anteriorly very wide phallus. There is however a discrepancy with the number of spurs on the hindtibia in the two species, a character that appears to hold true for every other Chrysopolomidae genus. *Diquishia morion* was said to possess one pair of spurs (Kurshakov & Zolotuhin 2016) yet *D. ansorgei* has two pairs. Based on the photograph of the hind leg of *D. morion* in Kurshakov & Zolotuhin (2016), the tarsi are broken off and it could be surmised that the second pair of spurs may have been damaged and lost. Several individuals of other genera with two pairs of tibial spurs examined as part of this study were observed to possess only three spurs or one pair on one tibia but two pairs on the other, suggesting that at least in pinned museum specimens, these spurs do break off. Although it is unlikely that these two species have different spur formulae, without any further material of *D. morion* it is difficult to come to a confident conclusion with regard this matter.

Distribution. The two species in this genus are restricted to Angola.

Species content

D. morion Kurshakov & Zolotuhin, 2016
D. ansorgei (Bethune-Baker, 1911)

Auripoloma gen. n.

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Figs 23, 42

Type species. *Chrysopoloma nigrociliata* Aurivillius, 1905

Syntypes. 1 ♂, 1 ♀.

Type locality. Hossere Miringi [Nigeria] (MfN).

Genus description. Medium size. Antennae bipectinate, scaling along flagellum yellow in basal third and then dark grey distally. Ground colour of thorax and abdomen beige; head and collar golden. Forewing broad, rounded, grey/silver in basal half and beige distally with straight, dark brown postmedial line, sometimes gently concave along the Cu veins. Small black scale spots along costal margin giving a speckled appearance up to postmedial line. Costal margin golden; fringe long, golden slightly darker than ground colour. Hindwing yellow-beige, fringe long, golden, slightly scalloped towards anal margin; distal portion of cilia black between vein M1 and the anal margin. Underside. Ground colour and legs golden; hindtibia with two pairs of spurs. Both wings beige, with faint postmedial line on hindwing which is slightly expanded towards costal margin; indistinct black scaling along costal margin. Male genitalia. Posterior process of transtilla medially split forming two, relatively thick, apically rounded processes; anterior process of transtilla very broad, apically hammerhead-shaped. Valve very wide, short, gradually tapering, distally rounded with slight concavity on distal edge. Juxta strongly sclerotised, square, with two rounded lateral processes and longer, central process. Phallus relatively short, strongly sclerotised and ridged distally, with short membranous vesica.

Diagnosis. At first glance, the single species of *Auripoloma* with its forewing postmedial line is somewhat reminiscent of *Scotinocerides* species but it is considerably smaller in size and the black fringe near the anal margin is distinctive. In the male genitalia, the *Auripoloma* species possesses a very large, broad transtilla which is apically hammer-head shaped, the valve is much wider at the base and the gnathos lobes are narrower and not fused apically.

Distribution. The single known species of this genus is distributed in the forest-savanna mosaics of West and northern Central Africa.

Etymology. This genus is dedicated to the Swedish entomologist Christopher Aurivillius, who described the family Chrysopolomidae after noticing that *Chrysopoloma* could not be placed in either Lasiocampidae or Limacodidae, and further added ten distinct taxa to the family including the only known species of this genus. The suffix 'poloma' is maintained in reference to *Chrysopoloma*, the genus from which the family name is formed.

Species content

A. nigrociliata (Aurivillius, 1905) comb. n.

Conclusion

This review inferred from phylogenetic and morphological investigations has updated the taxonomy and nomenclature of the Chrysopolomidae thus providing a baseline for future revisional works. It has been shown that the family consists of two distinct and well-supported lineages, the subfamilies Chrysopolominae and Ectropinae, and the true position of the genera *Achrocerides*, *Diqu-*

ishia, and *Strigivenifera* within the Chrysopolominae has been rectified.

It is worth noting that *Diquishia* and *Vietteopoloma* could not be sampled for the phylogenetic analyses and thus taxon sampling was incomplete; both genera could however confidently be placed in Chrysopolominae and Ectropinae respectively based on morphology. A further limitation was the analyses of only the COI-5P gene fragment with the addition of further gene regions likely to improve the resolution of the phylogeny. However, family-level phylogenetic inferences based on barcodes in other inset groups have been shown to be largely congruent with multi-loci analyses (Ptaszyńska et al. 2012) and the results in the present study are in the most part strongly supported by morphological characters of the genitalia.

The paradox of differing numbers of spurs on the hindtibia in the congeneric *Diquishia morion* and *D. ansorgei* also requires further investigation, this character having been shown to be unreliable at tribal level but consistent in every other genus in the family.

It will be of great interest to study the genital musculature of true Ectropinae species to see whether there are significant differences from Chrysopolominae which would add further support to the results presented in this study. Although beyond the scope of this work, a full revision of the genus *Chrysopoloma* is much-needed given the high levels of phenotypic variation observed throughout this group and it is believed that there are currently more names than species. In addition, further work is needed on the female Chrysopolomidae to determine what, if any, diagnostic characters they may possess.

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Research article

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Two new thermophilic species of the plant bug genus *Plagiognathus* from Japan and Taiwan (Hemiptera: Heteroptera: Miridae)

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Abstract. Two new species of the Holarctic phyline plant bug genus *Plagiognathus* Fieber, 1858 are described from Japan and Taiwan, namely *Plagiognathus marinoccidens* sp. nov. (Japan) and *P. chengshingi* sp. nov. (Taiwan). They are uniquely inhabiting warm temperate or subtropical climatic zones, unusual for the generally temperate distribution. The present finding also represents the first distributional record of the genus from Taiwan, the northeastern Oriental Region. A brief note on biology, food-preference, oviposition behavior and immature forms for *P. marinoccidens* is given. A key and checklist are provided to aid in identification and recognition of all known *Plagiognathus* congeners from Japan and Taiwan.

Key words. Phylinae, *Plagiognathus*, new species, Japan, Taiwan, key, SEM documentation.

INTRODUCTION

Plagiognathus Fieber, 1858 (tribe Phylini: subtribe Oncotylina) is a large Holarctic genus, comprising approximately 120 valid species (Schuh 2001; 2002–2013). The majority occur in the Nearctic Region and twenty-three species are currently known from the Palearctic Region (Aukema, 2018). Five species have been reported from Japan (Yasunaga, 2001; 2022), whereas no reliable record has been associated with Taiwan, the northeasternmost area of the Oriental Region.

During my continuing effort to update the phyline fauna of the eastern Asia, after a series of recent works (e.g., Yasunaga & Duwal 2019, 2021; Yasunaga et al. 2019, 2021; Yasunaga 2021, 2022), two undescribed species undoubtedly belonging to *Plagiognathus* have been confirmed. One species inhabits Japanese hop, *Humulus japonicus* (Cannabaceae) and was previously regarded as a thermophilic or vernal variant of *P. amurensis* Reuter (Yasunaga & Takai 2016); the other was collected from central Taiwan, or subtropical climatic zone (available specimens kept in the collection of National Museum of Natural Science, Taiwan). These species, *Plagiognathus marinoccidens* n. sp. (from Japan) and *P. chengshingi* n. sp. (Taiwan), are accordingly diagnosed and described in the present paper. The biology, food-preference, oviposition and immature forms observed for *P. marinoccidens* are briefly documented. A key is also provided to aid in identification of the Japanese and Taiwanese congeners. Scanning electron micrographs are shown for all treated taxa.

MATERIAL AND METHODS

Matrix code labels, which uniquely identify each specimen and are referred to as 'unique specimen identifier' (USI), are attached to the holotypes and some representative specimens. The USI codes [e.g., AMNH_PBI 0012345] comprise an institution and project code (AMNH_PBI) and a unique number (0012345). These specimens are searchable (by species name) on 'Heteroptera Species Pages' (http://research.amnh.org/pbi/heteropteraspeciespage/).

Rearing methodology mainly followed Fukuda et al. (2020) and Miyazaki et al. (2020); dried brine-shrimp eggs were placed on a folded tissue paper immersed with diluted fermented milk beverage in an acrylic container (110L × 85W × 35D mm), along with a few pieces of the host plant stem-vines (Fig. 3E–F).

Terminology mainly follows several comprehensive works treating phyline taxa (e.g., Schuh 1984; Menard et al. 2014; Schwartz et al. 2018; Yasunaga 2022). Synonymic lists for known taxa are omitted, as several comprehensive catalogs (including searchable online versions) are now available (Schuh 1995; Kerzhner & Josifov 1999; Schuh 2002–2013 online catalog; Aukema et al. 2013; Aukema 2018 online catalog). The suprageneric classification system for the subfamily Phylinae follows Schuh & Menard (2013) and Menard et al. (2014).

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Measurements are given in millimeters; for some of the SEM images, scale bars are shown in micrometers (µm). Scanning electron micrographs were taken with Hitachi Miniscope® (TM 4000II); the genitalic structures were also observed using a Nikon Eclipse Ci upright microscope, with a Photophase-Unit. For SEM documentation of the male and female genitalic structures, the delicate minute organs were dipped and washed in 60–70% ethyl alcohol after dissection under Olympus SZX-12 binocular stereoscopic microscope, placed on filter paper until dry, carefully attached to cards (ca. 5 × 15 mm) using water soluble wood glue, and finally placed in the SEM chamber for examination (without vapor deposition of metals).

Institutional abberviations

AMNH = American Museum of Natural History, New York, USA
CNC = Canadian National Collection of Insects, Ottawa, Ontario
NBIC = Nagasaki Biopark (Zoo) Insect Collection, Saikai, Japan
NMNS = National Museum of Natural Science, Taichung, Taiwan
TYCN = T. Yasunaga Collection, Nagasaki, Japan.

Abbreviations for morphological structures

Male genitalia
FS = field of stiff setae
GP = secondary gonopore
HP = hypophysis (apical parts of parameres)
LP = left paramere
PB = primary blade (of vesical appendage)
PT = phallotheca
RP = right paramere
SB = sensory lobe

Female genitalia
IRS = interramal sclerite
LOV = lateral oviduct
PMS = posterior margin sclerite (on interramal sclerite)
SCR = sclerotized ring
SPG = spermathecal gland.

Checklist of *Plagiognathus* in Japan and Taiwan

Subfamily Phylinae Douglas & Scott 1865
Tribe Phylini Douglas & Scott, 1865
Subtribe Oncotylina Douglas & Scott, 1865
Genus *Plagiognathus* Fieber 1858

P. amurensis Reuter, 1883 (Figs 1F–G, 2H–I, 3K–L, 4, 5I–L, 6A–D, 7D, 9J–O) – Distribution: Japan (Honshu, Shikoku), continental China and Russian Far East, Korea – Host: *Humulus japonicus* Sieb. & Zucc. (Cannabaceae), mostly on inflorescences both in Japan and Korea (Yasunaga 2001; Duwal et al. 2010; Yasunaga & Takai 2016), *Artemisia vulgaris* (Asteraceae) (Kerzhner 1988).

P. chengshingi Yasunaga sp. nov. – Taiwan (Nantou, Taichung) – Unknown.

P. chrysanthemi (Wolff, 1804) (Figs 2E, 4) – Japan (Hokkaido, Chishima Islands); known widely from the Holarctic Region (e.g., Wheeler & Henry 1992; Yasunaga 2001) – *Artemisia* spp. (Asteraceae), *Trifolium* spp. and *Vicia cracca* L. (Fabaceae), etc. (Kerzhner 1988; Yasunaga 2001).

P. collaris (Matsumura, 1911) (Figs 2F–G, 4) – Japan (Hokkaido, Honshu, Chishima Islands), NE China, Korean Peninsula, Russian Far East including Magadan and Sakhalin – polyphagous species; in northern Japan, known to be associated with *Artemisia* spp., *Filipendula camtschatica* (Pall.) Maxim. (Rosaceae) and *Vicia cracca* L. (Fabaceae). (Yasunaga 2001).

P. marinoccidens Yasunaga sp. nov. – Japan (Kyushu: Nagasaki Prefecture) – *Humulus japonicus* (young leaves, stem-vines and inflorescences); frequent predation on aphids was observed.

P. pini Vinokurov, 1978 (Figs 2K, 4) – Japan (Hokkaido, Chishima Islands), Russia (Primorsky Territory, Sakhalin and Yakutia) – *Pinus pumila* (Pall.) Regel (Pinaceae) (Kerzhner 1988; Yasunaga 2001).

P. yomogi Miyamoto, 1969 (Figs 1J–L, 2J, 4, 5M–O, 7C, 8H–O) – Japan (Hokkaido, Honshu, Shikoku, Kyushu), Korea, Russia (Primorsky Territory) – *Artemisia* spp. (Miyamoto 1969; Yasunaga 1999).

TAXONOMY

Plagiognathus Fieber, 1858

Diagnosis. East Asian congeners of *Plagiognathus* are recognized by the following combination of characters: Body elongate and subparallel-sided (♂)/ elongate-ovoid (♀), small to moderate in size (total length 2.9–4.5 mm); coloration variable (Figs 1–2); dorsum generally shining, with uniformly distributed, dark, simple setae, lacking silvery or wooly recumbent setae; vesica always with two apical blades (cf. Figs 6, 8B–C, 9D–F); sclerotized rings large, contiguous to each other mesally (Fig. 7); and posterior wall of bursae simple (cf. Figs 8E–F, 9H–I). As suggested by Schuh (2001), this large Holarctic genus is defined principally by the form of the male genitalia, such as twisted, often sigmoid vesica with two apical blades and rather slender, lanceolate right paramere. Some species of *Plagiognathus* exhibit great similarity in external appearance to certain members of *Europiella* Reuter, 1909; however, *Europiella* is distinct in having both silvery and simple setae on dorsum, right paramere remarkably widened and often squared, vesica apically with membranous area, and sclerotized ring small and narrow-rimmed (e.g., Schuh et al. 1995; Yasunaga 2022). Further diagnostic characters and a redescription for *Plagionathus* were provided by Schuh (2001).

Discussion

Plagiognathus forms one of the largest genera among the plant bug subfamily Phylinae and is known to comprise more than 120 described species; of these about 80 % are Nearctic elements (Schuh 2001, 2002–2013; Aukema 2018). Nonetheless, more than a few species appear to be wrongly placed in *Plagiognathus* and require further verification by dissecting the male genitalia (Schuh 2001). For eastern Asia, six congeners were reported by Yasunaga (2001), in addition to *P. obscuriceps* (Stål, 1858) occurring in northern Russian Far East and eastern Siberia and associated with *Salix* spp. (Salicaceae) (Kerzhner 1988).

In Japan and adjacent regions, the fauna of *Plagiognathus* species has previously been the subject of several recent works, and the known congeners were considered to occur predominantly in the temperate or colder climatic zones (Duwal et al. 2016; Yasunaga & Takai 2016; Yasunaga 2022). Nonetheless, two uniquely thermophilic species (described below) are now confirmed from the warm temperate zone in southwestern Japan as well as subtropical zone in Taiwan.

As pointed out by Schuh (2001), many *Plagiognathus* species are host-specific and arboreal. However, most of the East Asian congeners were confirmed to be associated with dicot herbaceous plants (Yasunaga 2001; Duwal et al. 2016), except for *P. pini* (a specialist of the boreal creeping pine, *Pinus pumila*). Several members (e.g., *P. arbustorum*) were also documented to prey on aphids or psyllids (Wheeler 2001). A univoltine life cycle is assumed for these East Asian species, but collection records suggest that a new species from Taiwan, *P. chengshingi* sp. nov., may have two or more generations per year. Although Kerzhner (1988) reported *Artemisia vulgaris* (Asteraceae) as the host plant of *P. amurensis* in Russian Primorsky Territory, it does not appear the breeding host of this hop-inhabiting phyline (Yasunaga 2001; Duwal et al. 2010).

Key to species known in Japan and Taiwan

1. Head and pronotum wholly pale yellow-green (fading to pale brown or stramineous brown in dry-preserved specimens); antennal segment II pale brown, sometimes with dark extreme base [if body widely pale then antennal segment II uniformly darkened: pale variant of *P. yomogi* (cf. Fig. 1L)] .... ***P. chrysanthemi*** (Wolf, 1804)
– Head and at least anterior part of pronotum fuscous, brown or reddish brown; antennal segment uniformly darkened 2
2. Currently assumed to be endemic to Taiwan; ventral color pattern on metafemur as in Fig. 1C–E .... ***P. chengshingi*** sp. nov.
– Known from Japan (and temperate or colder climatic zones in China, Korea and Russian Far East) 3
3. Habitat restricted to *Pinus pumila* at alpine or boreal zone (currently restricted to Taisetsu Mountains in Hokkaido) .... ***P. pini*** Vinokurov, 1878
– Associated with herbs or shrubs of dicot angiosperms 4
4. Total body length more than 4 mm; dark spots on metafemur arranged in rows or sometimes partly fused (cf. Fig. 4) .... ***P. collaris*** Matsumura, 1911
– Body less than 4 mm (mostly < 3.7 mm) in total length; metafemoral dark spots distributed randomly 5
5. Antennal segment III as long as or shorter than head width across eyes; thermophilic species currently restricted to coastal zones of western Kyushu .... ***P. marinoccidens*** sp. nov.
– Antennal segment III longer than head width across eyes; known from temperate and cold temperate zones 6
6. Dorsum uniformly fuscous, shining; cuneus usually uniformly fuscous; metafemoral dark spots smaller, rather sparsely distributed; associated with *Artemisia* spp. ....***P. yomogi*** Miyamoto, 1969
– Dorsum not much shining, variable in color, pale brown or reddish brown [if dorsum widely darkened, then anterior and posterior margins of cuneus pale brown or yellow-orange]; anterior margin and apex of cuneus (sometimes whole cuneus) pale; dark spots on metafemur larger, densely distributed; *Humulus japonicus* .... ***P. amurensis*** Reuter, 1883

Plagiognathus chengshingi sp. nov.

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Figs 1A–E, 5A–D, 7A, 8A–F

Diagnosis. Based on the similarity in the general shape and the male genitalia, this new species is assumed to be most closely related to *P. yomogi* Miyamoto, from which *P. chengshingi* sp. nov. can be distinguished by the following characters: Generally paler general coloration; antennal segment III obviously shorter than width of head across eyes; profemur lacking dark stripe along anterior margin; smaller peritreme of metathoracic scent efferent system (Fig. 5B–C, vs 5N in *P. yomogi*); longer and slenderer apical blades of vesica (Fig. 8B–C, vs Fig. 8M–N); relatively narrow female sclerotized ring (Fig. 7A, vs Fig. 7C); and wider interramal sclerite laterally with sparsely distributed, comb-shaped microstructures (Fig. 8E, vs Fig. 8I).

Etymology. Named in honor of Dr Cheng Shing Lin, the former curator of NMNS, Taiwan, who contributed to clarification of the Taiwanese fauna of the Miridae as well as collected the specimens of this new species; a noun in the genitive case.

Type material

Holotype. TAIWAN – ♂; Taichung, Waipu, 24°20′ N, 120°41′ E, sweep-netting, 24 Aug. 2000, C. S. Lin and W. T. Wang (NMNS) (AMNH_PBI 00380758).

Paratypes (all deposited in NMNS). TAIWAN – 1 ♂, 1 ♀ (NMNS), same collection data as for holotype • 1 ♀, Nantou, Chichi, 23°50′ N, 120°48′ E, sweep-netting, 14 Mar 2002, C.S. Lin • 1 ♀; Nantou, Tungpu, 2000 m alt., 23°34′ N, 120°53′ E, 18–21 Sep 1981, T. Lin and W.S. Wang • 1 ♀, same locality as for preceding, 10–14 Jan. 1983, K.C. Chau and P. Huang.

Description

General shape not sexually dimorphic; female has slightly larger size, wider vertex and shorter antennal segment II (Table 1) as in many other phylines. Body elongate-ovoid, relatively small in size; basic coloration variable but usually dark brown; dorsal surface widely shiny dark brown (Fig. 1B), sometimes orange-brown (Fig. 1A), with uniformly distributed, brown, simple setae, lacking silvery setae (cf. Fig. 1B; dorsal vestiture shown in Fig. 5A rubbed off). Head usually shiny fuscous, with sparsely distributed, silky, upright setae; vertex pale orange-brown to castaneous brown; buccula usually yellowish brown. Antenna almost uniformly dark brown; male segment II about as long as basal width of pronotum; segment III and IV slightly lighter; segment III as long as or shorter than head width across eyes. Labium shiny pale reddish brown, about as long as metafemur; its apex reaching but not exceeding apex of mesocoxa; apical part of segment IV darkened. Pronotum, mesoscutum and scutellum shining, varying from reddish brown (Fig. 1A) to dark brown (Fig. 1B);

Table 1. Measurements for *Plagiognathus* species. Abbreviations: F = female; FM = femur; HT = holotype; L = length; LBM = labium; M = male; PRN = pronotum; PT = paratype; TB = tibia; VTX = vertex (interocular space); W = width; 1G = 1st annual generation; 2G = 2nd generation.

Plagiognathus		**Body**	**Head**	**VTX**	**PRN**	**Max**	**Antennomere L**				**LBM**	**Metaleg L**	
		L	W	W	W	W	I	II	III	IV	L	FM	TB
chengshingi	HT M	**3.11**	**0.71**	**0.33**	**1.05**	**1.26**	**0.29**	**1.05**	**0.65**	**0.41**	**1.20**	**1.20**	**1.73**
M (N = 3)	PT M	3.19	0.69	0.33	1.04	1.28	0.29	1.05	0.66	–	1.25	1.20	1.71
	PT M	3.06	0.64	0.32	0.95	1.16	0.27	1.02	0.65	0.41	1.17	1.08	1.58
	PT F	3.33	0.71	0.36	1.07	1.38	0.29	0.86	0.62	0.39	1.23	1.20	1.67
F (N=3)	PT F	3.26	0.71	0.38	1.05	1.35	0.27	0.87	0.59	0.44	1.25	1.20	1.65
	PT F	3.19	0.72	0.36	1.10	1.35	0.27	1.04	–	–	1.26	1.26	1.80
***marinoccidens* (1G)**	MAX	3.19	0.69	0.33	0.99	1.20	0.26	0.98	0.63	0.47	1.20	1.14	1.68
M (N = 3)	MIN	2.94	0.65	0.32	0.92	1.14	0.21	0.95	0.62	0.33	1.11	1.07	1.64
	MEAN	**3.09**	**0.67**	**0.32**	**0.96**	**1.17**	**0.23**	**0.96**	**0.62**	**0.41**	**1.15**	**1.10**	**1.66**
	MAX	3.43	0.73	0.38	1.16	1.47	0.30	0.95	0.75	0.54	1.26	1.20	1.82
F (N = 5)	MIN	2.94	0.69	0.33	1.05	1.35	0.24	0.84	0.59	0.32	1.10	1.05	1.70
	MEAN	**3.21**	**0.71**	**0.36**	**1.09**	**1.41**	**0.27**	**0.90**	**0.66**	**0.44**	**1.19**	**1.16**	**1.74**
***marinoccidens* (2G)**	MAX	3.48	0.75	0.36	1.17	1.46	0.30	1.20	0.75	0.50	1.29	1.34	1.91
M (N = 3)	MIN	3.01	0.69	0.32	1.02	1.32	0.27	1.05	0.69	0.47	1.20	1.20	1.71
	MEAN	**3.29**	**0.72**	**0.34**	**1.11**	**1.38**	**0.28**	**1.13**	**0.74**	**0.48**	**1.23**	**1.24**	**1.83**
	MAX	3.70	0.77	0.42	1.25	1.64	0.30	1.19	0.75	0.47	1.35	1.34	1.95
F (N = 5)	MIN	2.96	0.66	0.35	1.04	1.38	0.26	0.81	0.60	0.38	1.10	1.16	1.65
	MEAN	**3.46**	**0.72**	**0.39**	**1.19**	**1.55**	**0.29**	**1.02**	**0.68**	**0.44**	**1.27**	**1.28**	**1.84**
amurensis	MAX	4.09	0.75	0.36	1.23	1.50	0.33	1.29	0.87	0.56	1.38	1.38	2.10
M (N = 6)	MIN	3.19	0.71	0.33	1.05	1.31	0.26	1.14	0.75	0.42	1.20	1.25	1.85
	MEAN	**3.72**	**0.74**	**0.35**	**1.17**	**1.42**	**0.30**	**1.22**	**0.81**	**0.49**	**1.31**	**1.34**	**2.00**
	MAX	3.92	0.75	0.41	1.29	1.65	0.32	1.13	0.80	0.50	1.40	1.43	2.10
F (N = 5)	MIN	3.50	0.72	0.39	1.19	1.50	0.30	1.05	0.75	0.45	1.28	1.23	1.85
	MEAN	**3.69**	**0.74**	**0.40**	**1.25**	**1.61**	**0.30**	**1.07**	**0.77**	**0.47**	**1.34**	**1.34**	**1.97**
yomogi	MAX	3.36	0.69	0.33	1.07	1.34	0.29	1.08	0.75	0.48	1.22	1.23	1.83
M (N = 4)	MIN	2.70	0.65	0.32	0.95	1.17	0.26	0.90	0.72	0.45	1.08	1.05	1.64
	MEAN	**3.12**	**0.66**	**0.33**	**1.01**	**1.26**	**0.27**	**1.00**	**0.73**	**0.46**	**1.18**	**1.17**	**1.73**
	MAX	3.26	0.71	0.38	1.11	1.43	0.29	0.99	0.74	0.50	1.28	1.28	1.85
F (N = 3)	MIN	3.01	0.65	0.36	1.01	1.40	0.26	0.93	0.71	0.47	1.20	1.23	1.80
	MEAN	**3.15**	**0.67**	**0.37**	**1.06**	**1.41**	**0.27**	**0.96**	**0.72**	**0.48**	**1.24**	**1.25**	**1.82**

scutellum shallowly and transversely rugose; thoracic pleura shining, varying from fuscous (Fig. 1C) to pale reddish brown with darkened parts (Fig. 1D); metathoracic scent efferent system yellowish brown, with small peritreme (Fig. 5B–C). Hemelytron variable in color as in pronotum; lateral margin of corium and basal and

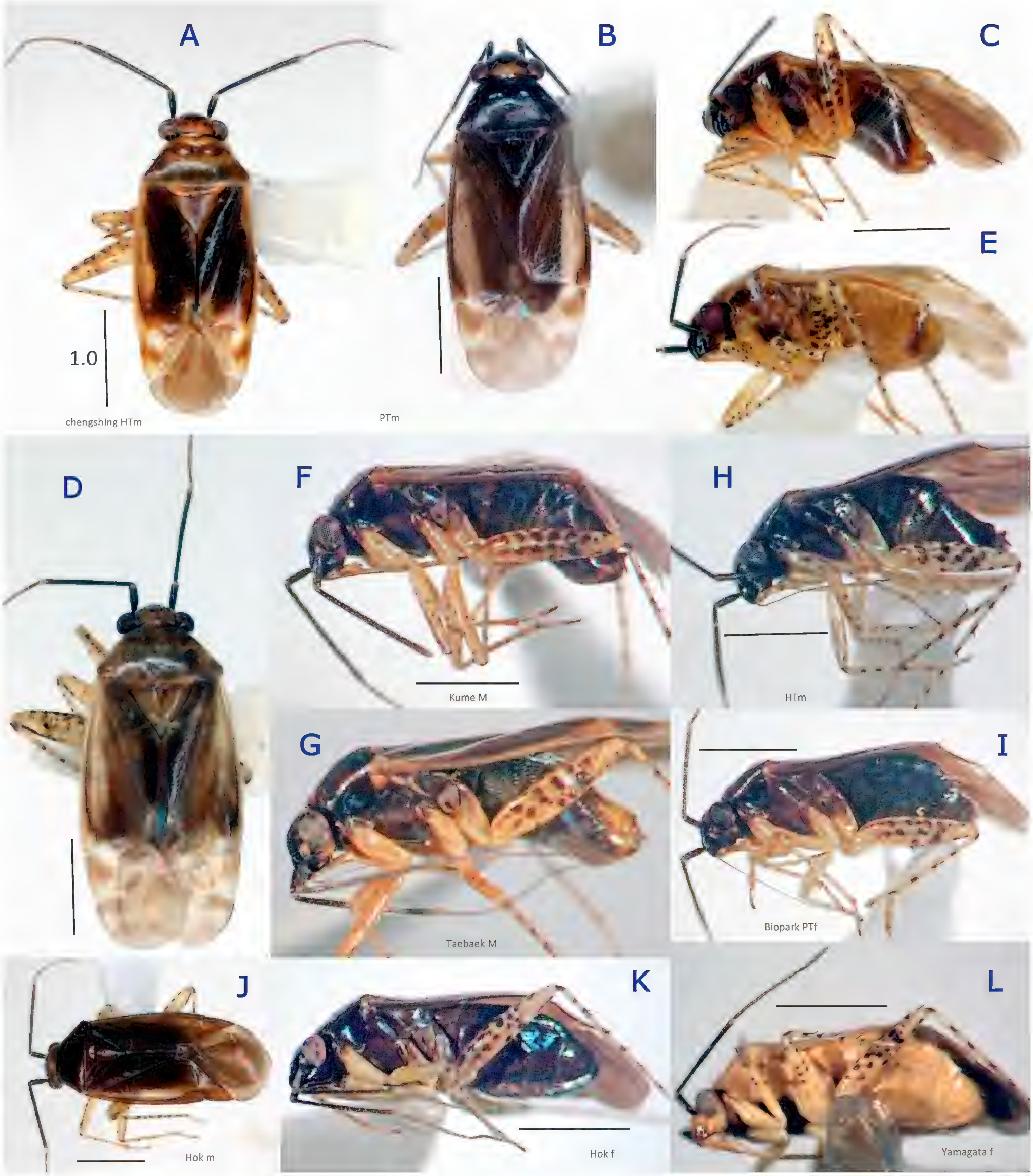

Fig. 1. Dorsal (A–B, D, J) and left lateral (C, E–I, K–L) habitus images of *Plagiognathus* spp. **A**. *P. chengshingi* sp. nov., holotype, ♂. **B–C**. *P. chengshingi* sp. nov., paratype, ♂. **D–E**. *P. chengshingi* sp. nov., paratype, ♀. **F**. *P. amurensis* from Kume Town, Okayama, Japan. **G**. *P. amurensis* from Taebaek, Kangwon-do, Korea. **H**. *P. marinoccidens* sp. nov., holotype, ♂. **I**. *P. marinoccidens* sp. nov.,paratype, ♀. **J**. *P. yomogi*, ♂ from Hokkaido, Japan. **K**. *P. yomogi*, ♀ from Hokkaido. **L**. *P. yomogi*, pale variant ♀ from Yamagata, Japan.

apical margins of cuneus usually pale; membrane pale smoky brown, semitransparent, with obscure maculae in large areolar cell and posterior to cuneal apex. All coxae yellowish brown, partly tinged with red; legs yellowish brown; each femur lacking dark stripe along anterior margin; pattern of ventral femoral spots as in Fig. 1C–E; metafemoral dark spots often fused; each tibia with a dark (knee) spot at joint with respective femur; each tarsomere III darkened; meta-tarsomere II slightly longer than III; pretarsal structure as in Fig. 5D; pulvilli relatively narrow. Abdomen shining, varying from pale brown to dark castaneous. Male genitalia (Fig. 8A–C): Right paramere relatively slender; phallotheca short, rather blunt-tipped (Fig. 8A); vesica sigmoid, with comparatively sharpened and elongate apical blades (Fig. 8B); longer (principal) blade slightly curved apically (Fig. 8C). Female genitalia (Figs 7A, 8D–G): Sclerotized ring rather narrow and small (Figs 7A, 8D); posterior wall relatively smooth (Fig 8F); interramal sclerite laterally with sparsely distributed, comb-like microstructures (Fig. 8E); apex of ovipositor (gonapophysis) I rather densely serrate (Fig. 8G).

Measurements

See Table 1. Holotype male: Total body length 3.11; head width across eyes 0.71; vertex width (interocular space) 0.33; lengths of antennal segments I–IV 0.29, 1.05, 0.65 and 0.41; total length of labium 1.20: basal width of pronotum 1.05; maximum width across hemelytra 1.26; and lengths of metafemur 1.20, tibia 1.73 and tarsus 0.41, respectively.

Biology

Unknown.

Plagiognathus marinoccidens sp. nov.

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Figs 1H–I, 2A–D, 3A–K, 4, 5E–H, 6E–H, 7B, 9A–I

Diagnosis. Recognized by its small size; generally fuscous body (Figs 2A–D, 3B); uniformly darkened head; short antennal segment II; relatively long labium that is longer than metafemur; relatively narrow peritreme of scent efferent system (Fig. 5G); creamy yellow femora and tibiae; rather stout, blunt-tipped phallotheca (Fig. 9B); short, slender apical blades of vesica (Fig. 6E–H, 9E–F); and relatively narrow interramal sclerite (Fig. 9H) with densely distributed, comb-like microstructures (Fig. 9I), in addition to unique thermophilic habitat preference. This new species is assumed to be sister to *P. amurensis*, from which *P. marinoccidens* sp. nov. can be distinguished by the characters mentioned in the above key (couplet 4), smaller size, generally fuscous basic coloration (Fig. 2A–D, vs 2H–I), slenderer vesical blades (Fig. 9E, vs 9O), smaller sclerotized rings (Fig. 9G, vs 9J), and more densely distributed microstructures on the narrower interramal sclerite (Fig. 9H–I, vs 9K–L). Paler color variant (Fig. 3C–D) was confirmed in the 2nd (autumn) generation females; however, only three of 43 specimens had the paler coloration, and extent of the pale grayish brown parts on the dorsum is rather restricted (Fig. 3C), by comparison with *P. amurensis* (Fig. 2I).

Plagiognathus marinoccidens sp. nov. is also externally very similar to *P. yomogi*, but this *Artemisia*-inhabiting phyline is allopatric (known from colder climatic zones) and has the following different features: antennal segment III longer than head width across eyes; anterior margin of profemur usually with a dark stripe; metafemur with sparser dark spots ventrally (Fig. 4); metathoracic scent efferent system triangular, with wider peritreme (Fig. 5N); phallotheca tapered and sharpened apically (Fig. 8L); vesical with thick primary blade (Fig. 8N); and inner half area of interramal sclerite smooth, lacking microstructures (Fig. 8J).

The nymphs (Figs 3H–K) of *P. marinoccidens* sp. nov. are recognized readily by the generally pale green coloration, annulated antennae and striped femora. The final instar nymph of the new species is very similar to that of *P. amurensis* (Fig. 3M); the former can be distinguished from the latter by the yellowish basic coloration, darkened apical ¼ of the antennal segment II and enlarged dark spots on the metatibia.

Etymology. From Latin, marinus (marine, of the sea) combined with occidens (west), referring to the restricted habitats of this new species along the westernmost coastal zone of Mainland Japan; an adjective.

Type material

Holotype. JAPAN – ♂ (AMNH) (AMNH_PBI 00380759), Kyushu, Nagasaki Pref., Nagasaki City, Kabashima Island, 32°33′22.2″ N, 129°46′39.2″ E, on *Humulus japonicus* (sweep-netting young leaves and stems), 15 Jun. 2013, T. Yasunaga.

Paratypes. JAPAN – 1 ♂, 1 ♀ (TYCN), same locality data as for holotype • 1 ♂ (TYCN), Nagasaki City, Kinkai-Tonehara (harbor), 32°54′04.1″ N, 129°47′42.1″ E, on *Humulus japonicus* (young leaves and stems), 2 Jun 2022, T. Yasunaga • 1 ♀ (TYCN), Nagasaki City, Kohno'ura-Ougiyama, 32°53′20.9″ N, 129°43′26.3″ E, UV lighting, 23 Jul. 2022, T. Yasunaga • 32 ♂♂, 13 ♀♀ (AMNH, NBIC, TYCN), Nagasaki City, Kohno'ura Harbor (Fig. 3A), 32°52′54.7″ N, 129°40′44.7″ E, on *Humulus japonicus* (inflorescences and leaves), 1 Oct 2022, T. Yasunaga • 8 ♂♂, 2 ♀♀ (TYCN) (4th or 5th instar nymphs when collected and reared with synthetic diet, then emerging on 3–5 Oct 2022) • 20 ♂♂, 22 ♀♀ (CNC, NMNS, TYCN) same collection data as for preceding • same collection data as for preceding, 8 Oct. 2022 • 2 ♂♂, 7 ♀♀ (3rd–5th instar nymphs when collected and reared, then emerging on 9–13 Oct. 2022, and 1♂ dead on Oct. 21, 1 ♀ on Oct. 30, 1 ♂, 3 ♀♀ on Nov. 5 and 3 ♀♀ on Nov. 6) (TYCN) • 17 ♂♂, 6 ♀♀ (AMNH, TYCN), same collection data

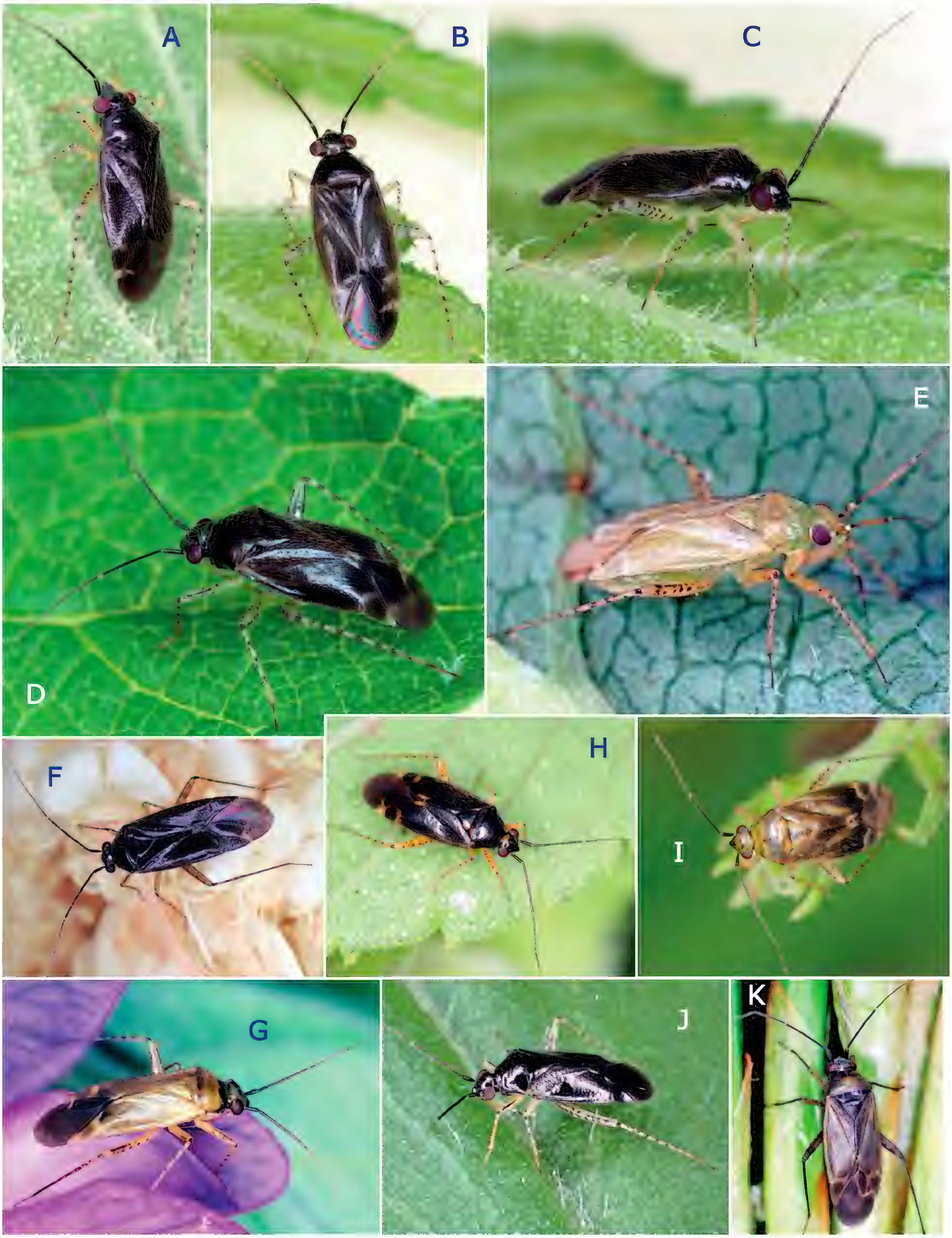

Fig. 2. Habitus images of living individuals of Japanese *Plagiognathus* spp. **A–B**. *P. marinoccidens* sp. nov., ♂. **C–D**. .*P. marinoccidens* sp. nov., ♀. **D**. *P. marinoccidens* sp. nov., ♀. **E**. *P. chrysanthemi*, ♀. **F**. *P. collaris*, ♂. **G**. *P. collaris*, ♂, pale variant. **H**. *P. yomogi*, ♂. **I**. *P. yomogi*, ♀. **J**. *P. yomogi*, ♂. **K**. *P. pini*, ♂. H–I. Courtesy of M. Takai.

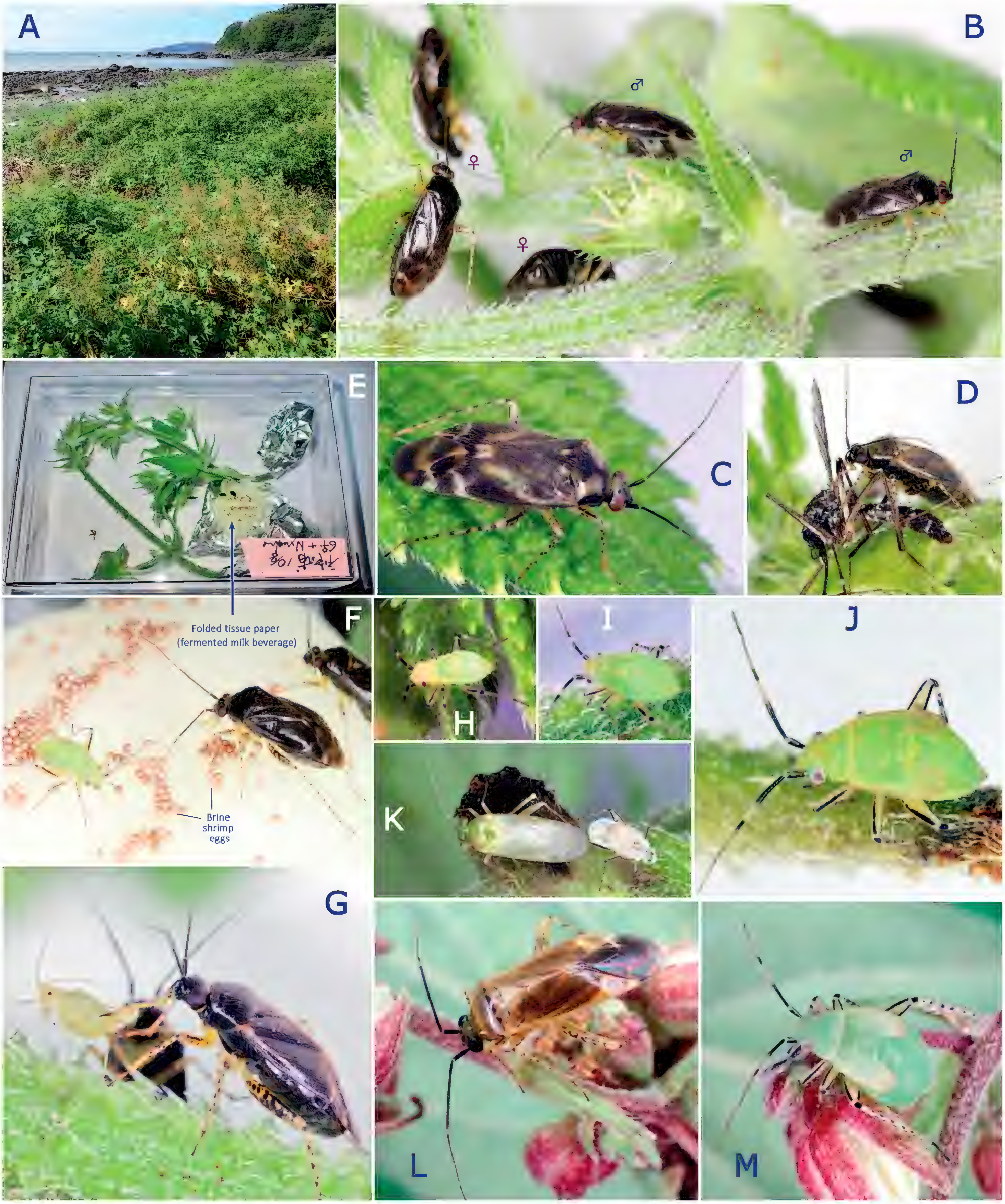

Fig. 3. Habitat and habitus images of living individuals of *Plagiognathus marinoccidens* sp. nov. (B–K, the 2nd generation collected at Fig. A, with reared samples, F–K) and *P. amurensis* (L–M, from Suwon, Korea). **A**. Vegetation of *Humulus japonicus* at sandy beach in Nagasaki, Japan, habitat of *P. marinoccidens* sp. nov. **B**. Adults on the breeding host. **C**. Paler variant ♀. **D**. Same, scavenging on cadaver of a mosquito, *Aedes albopictus*. **E**. Rearing kit with pieces of the host plant and synthetic diet. **F**. Adults and 5th instar nymph (left) feeding on synthetic diet. **G**. A female preying on an aphid. **H**. First instar nymph. **I**. Third instar. **J**. Final instar. **K**. Unpigmented adult ♂, just completing eclosion. **L**. Adult ♂, with orange-brown dorsum. **M**. Final instar nymph.

as for preceding, 12 Nov. 2022 • 1 ♂, 2 ♀♀ (NBIC, TYCN), Nagasaki Pref., Saikai City, Seihi Town, Nagasaki Biopark (Zoo), 32°59′19″ N, 129°47′14″ E, UV lighting, 20 Jun. 2013, T. Yasunaga.

Description

General shape not sexually dimorphic; female has slightly larger size, wider vertex and shorter antennal segment II (Table 1) as in above new species; color variation not significant but body partly pale grayish brown in 2nd (autumn) generation female as in Fig. 2A–D; 2nd generation slightly larger than the 1st (Table 1). Body rather elongate, subparallel-sided, small-sized; basic coloration fuscous (pale variant rarely present in 2nd generation female, with partly grayish brown head, pronotum, lateral margins of scutellum, posterior part of clavus and ventral posterior part of abdomen, cf. Fig. 3C–D); dorsal surface widely shiny fuscous (Fig. 2A–D), with uniformly distributed, pale, simple setae, lacking silvery setae (Figs 2A–D, 3C, G, 5D). Head, including vertex and frons, shiny fuscous, with sparsely distributed, pale, upright setae. Antenna almost uniformly dark brown; male segment II about as long as basal width of pronotum; segment III and IV whitish in fresh specimens (e.g., Fig. 2B); segment III as long as or shorter than head width across eyes. Labium shiny creamy yellow, longer than metafemur; its apex slightly surpassing apex of mesocoxa; apical half of segment IV dark reddish brown. Pronotum, mesoscutum and scutellum uniformly fuscous, shining; scutellum flat; thoracic pleura almost uniformly darkened (Fig. 1H–I); metathoracic scent efferent system dark brown, with small, narrow peritreme (Fig. 5G). Hemelytron uniformly shiny fuscous, except for basal margin and apex of cuneus pale; membrane smoky brown, with posteriorly whitish vein. All coxae creamy yellow, with more or less darkened bases; legs creamy yellow; each femur without noticeable dark stripe along anterior margin; pattern of ventral femoral spots as in Figs 1H–I, 4; metafemoral dark spots generally smaller than those of *P. amurensis* (cf. Figs 1F–G, 4); each tibia with a dark (knee) spot at joint with respective femur; apex of each tarsomere III darkened; pretarsal structure as in Fig. 5H; claws rather slender and sharpened, with pulvilli somewhat widened

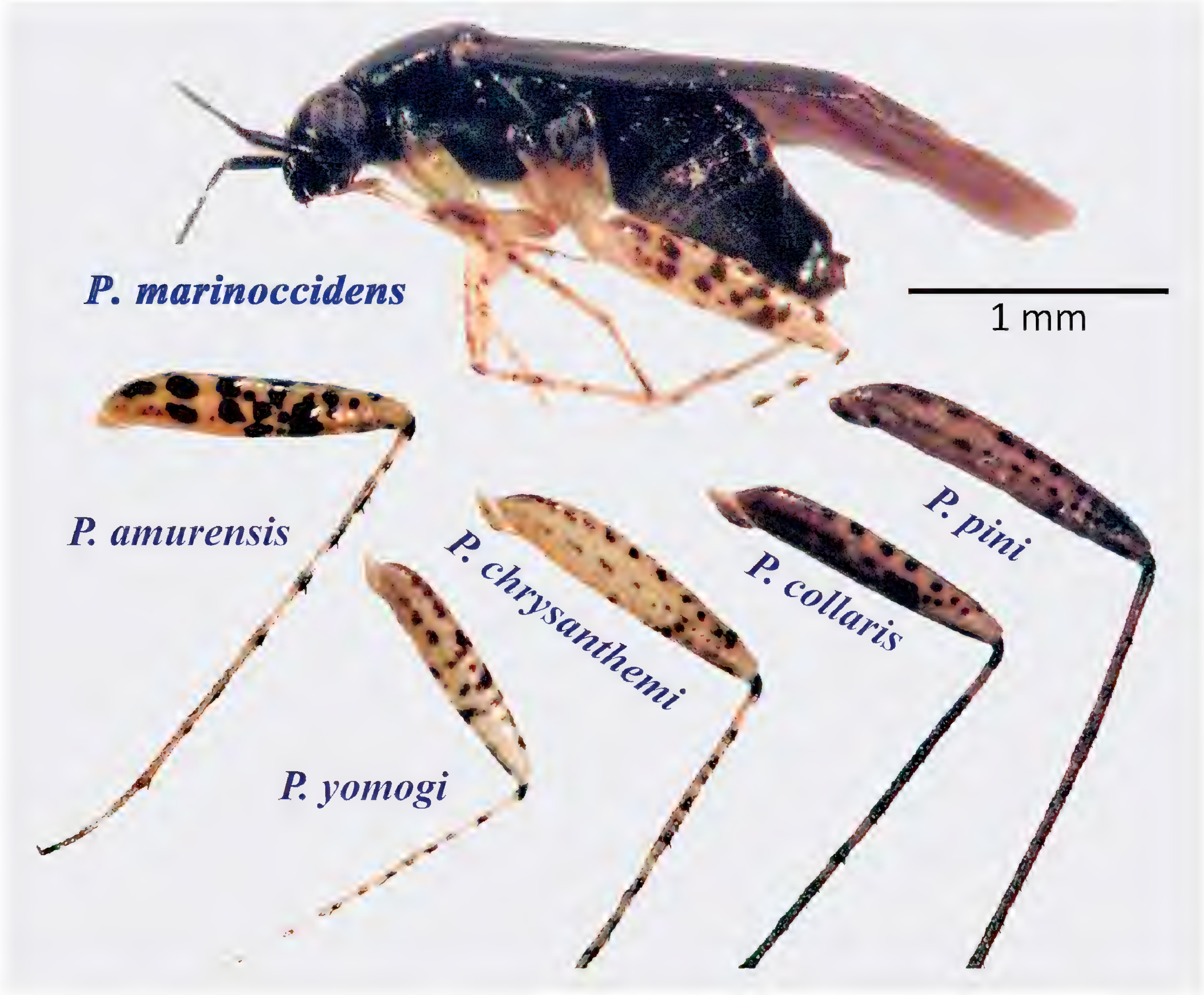

Fig. 4. Metafemoral ventral dark spot pattern of six Japanese *Plagiognathus* spp.

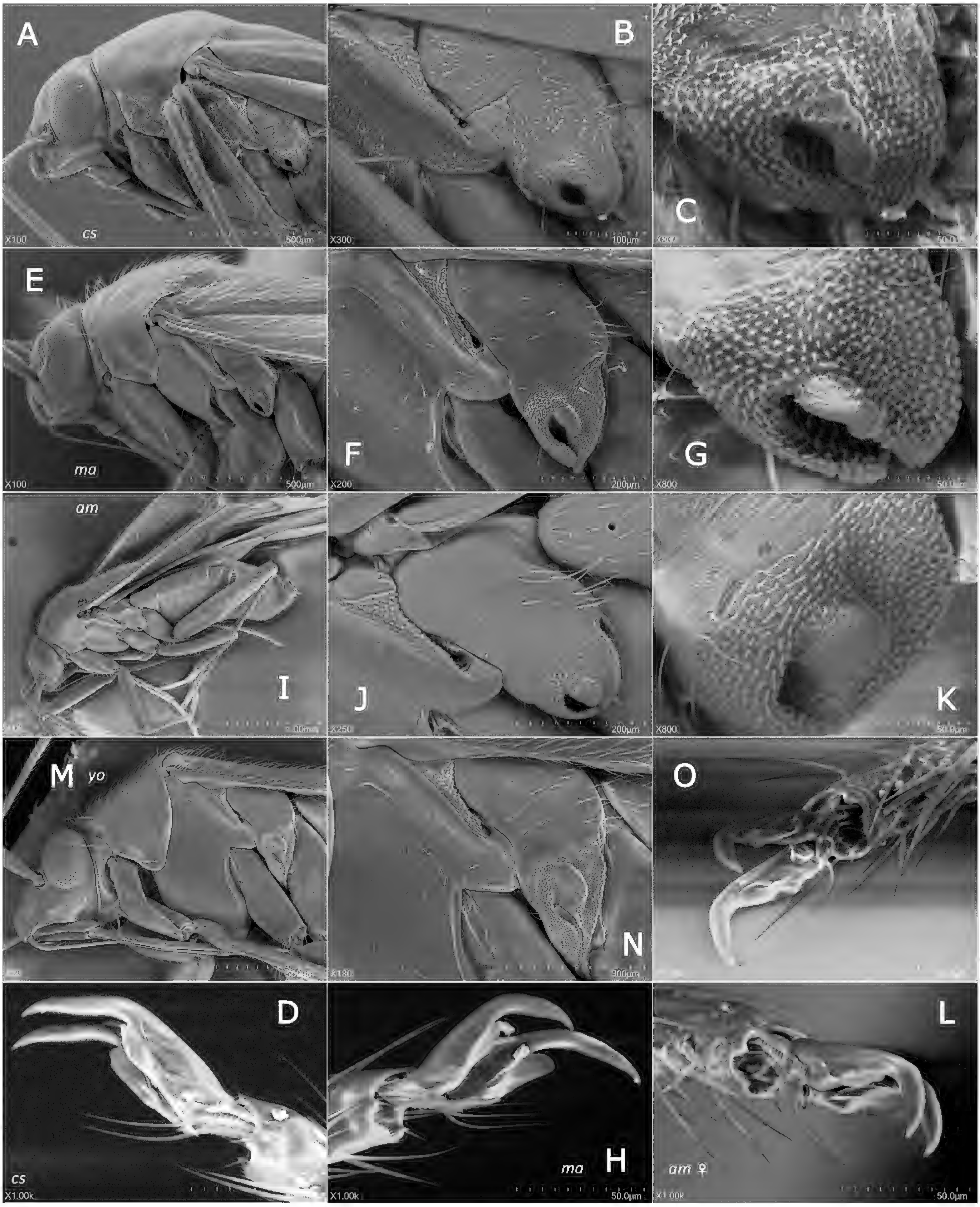

Fig. 5. **A–D**. Scanning electron micrographs for *Plagiognathus chengshingi* sp. nov. **E–H**. *P. marinoccidens* sp. nov. **I–L**. *P. amurensis*. **M–O**. *P. yomogi*. **A, E, I, M**. Left lateral habitus. **B, F, J, N**. Thoracic pleura, left lateral view. **C, G, K**. Metathoracic scent efferent system. Ventral habitus. **D, H, L, O**. Pretarsal structure of metaleg.

towards apex. Abdomen almost entirely shiny fuscous in both sexes. Male genitalia (Figs 6E–H, 9A–F): Right paramere relatively wide, somewhat flattened (Fig. 9A); hypophysis of left paramere sub-triangular (Fig. 9C); phallotheca rather stout, blunt-tipped (Fig. 9B); vesica sigmoid but not coiled, with short, slender apical blades that are not thickened basally (Figs 6E–H, 9E–F). Female genitalia (Figs 7B, 9G–I): Sclerotized ring rather small, with thicker anterior margin (Figs 7B, 9G); posterior wall relatively narrow (Fig 9H); interramal sclerite (except for its smooth inner corner) with densely distributed, comb-like microstructures (Fig. 9I).

Measurements

See Table 1. Holotype male: Total body length 3.19; head width across eyes 0.68; vertex width (interocular space) 0.33; lengths of antennal segments I–IV 0.21, 0.95, 0.63 and 0.33; total length of labium 1.20: basal width of pro-

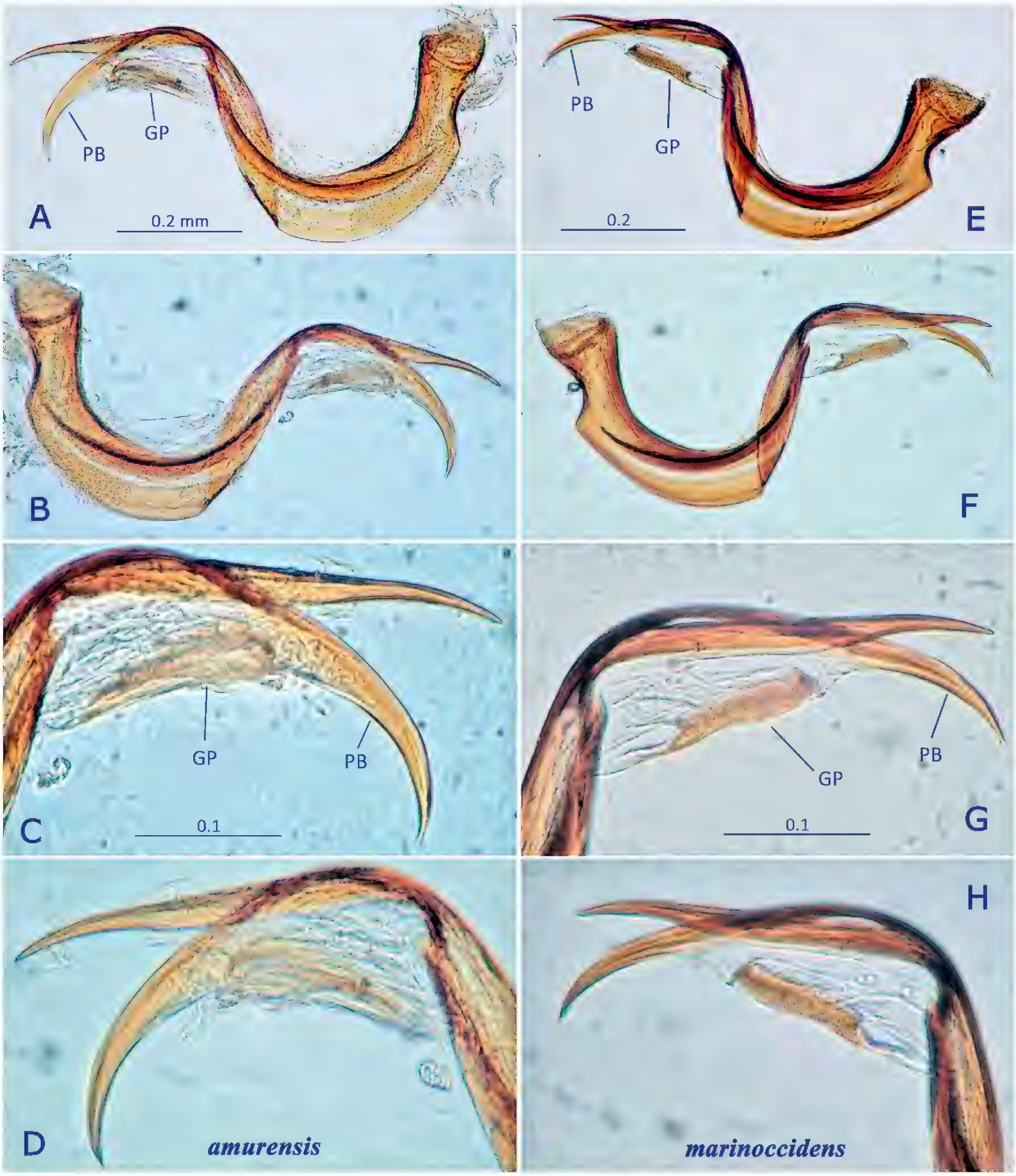

Fig. 6. A–D. Male genitalia (vesica) of *Plagiognathus amurensis* from Suwon, Korea. **E–H**. *P. marinoccidens* sp. nov. from Nagasaki, Japan. Abbreviations: see Material and methods.

notum 0.99; maximum width across hemelytra 1.20; and lengths of metafemur 1.08, tibia 1.68 and tarsus 0.47, respectively.

Biology

The breeding host of this new bivoltine species was confirmed as a Japanese wild hop, *Humulus japonicus*. The immature forms of the 2nd (autumn) generation were recently discovered (Fig. 3A–H), and the newly emerged adults of the 1st generation (cf. Fig. 2B) were collected from young leaves and stem vines of the host in early summer. The adults were occasionally attracted to UV light at night. Both of *Plagiognathus marinoccidens* sp. nov. and its assumed closest sibling, or *P. amurensis*, are associated with the same plant species. However, the latter seems to have a univoltine life cycle, as both of the adults and nymphs of Japanese population were only found between late August to late October (Yasunaga 2001; Yasunaga &

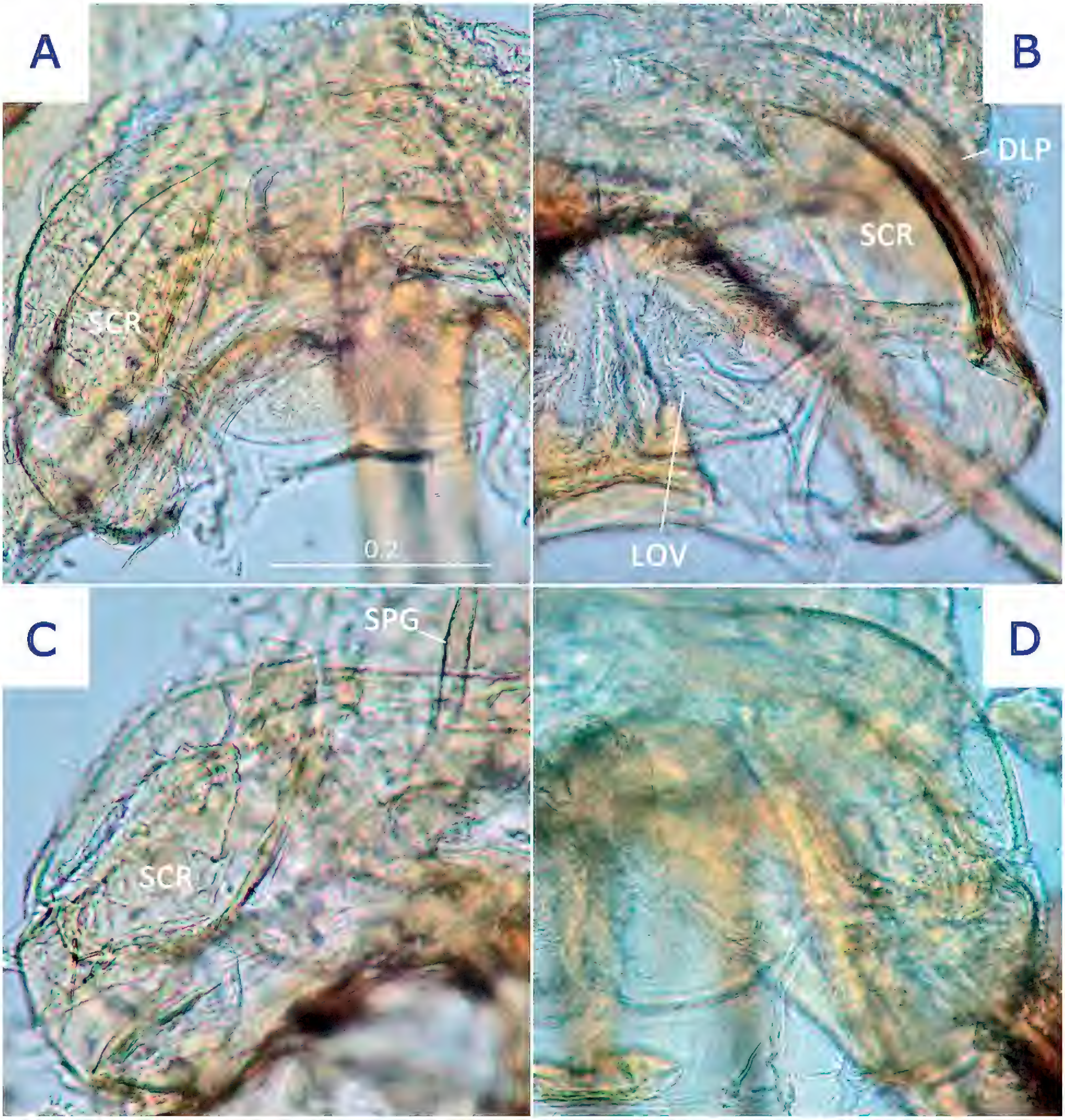

Fig. 7. Female genital chamber of *Plagiognathus* spp. in dorsal view. **A**. *P. chengshingi* sp. nov. **B**. *P. marinoccidens* sp. nov. **C**. *P. yomogi*. **D**. *P. amurensis*. Abbreviations: see Material and methods.

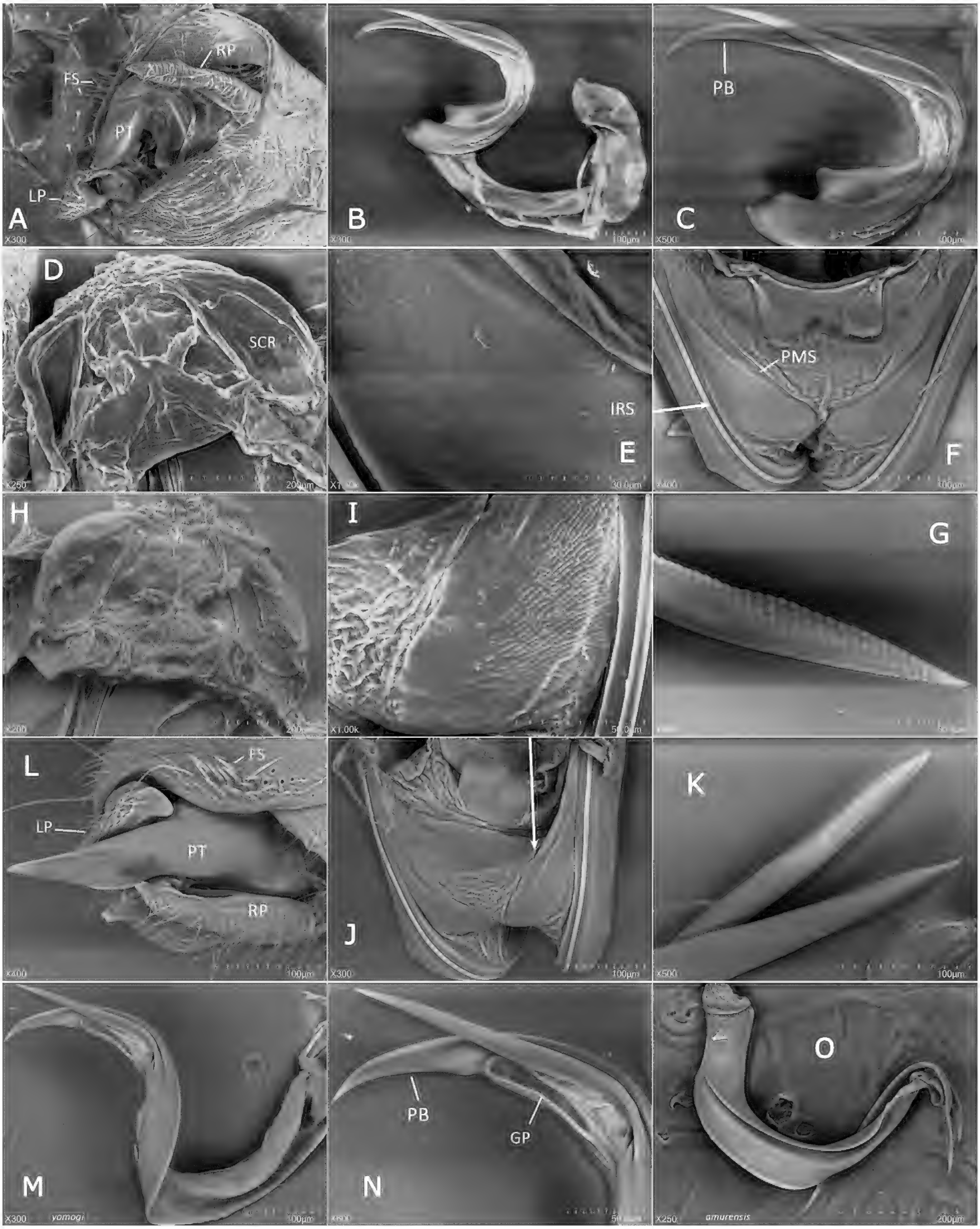

Fig. 8. A–C, L–O. Scanning electron micrographs of ♂ genitalia. **D–K**. Scanning electron micrographs of ♀ genitalia. **A–G**. *Plagiognathus chengshingi* sp. nov. **H–N**. *P. yomogi*. **O**. *P. amurensis*. **A, L**. Genital segment (pygophore) with phallotheca and parameres, dorsal view. **B–C, M–O**. Vesica. **D, H**. Genital chamber, dorsal view. **E–F, I–J**. Posterior wall. **G, K**. Apex of ovipositor (gonapophysis I). Abbreviations: see Material and methods.

Takai 2016), and the distributions of the two species are obviously disjunct from one another. Along coastal zones of Nagasaki Prefecture, the Japanese hop (often regarded as a rampant weed) grows everywhere. Nonetheless, the habitats of *P. marinocciden* are obviously restricted. Although I have carefully searched this bug at more than 20 sites for the past couple of years, only five collecting sites mentioned in the above type material section have hitherto yielded specimens. The adults of the second (autumn) generation occurring at Kohno'ura Harbor of Nagasaki City (Fig. 3A, 32°52′54.7″ N, 129°40′44.7″ E) were observed to survive until early November when the host plant starts to wither.

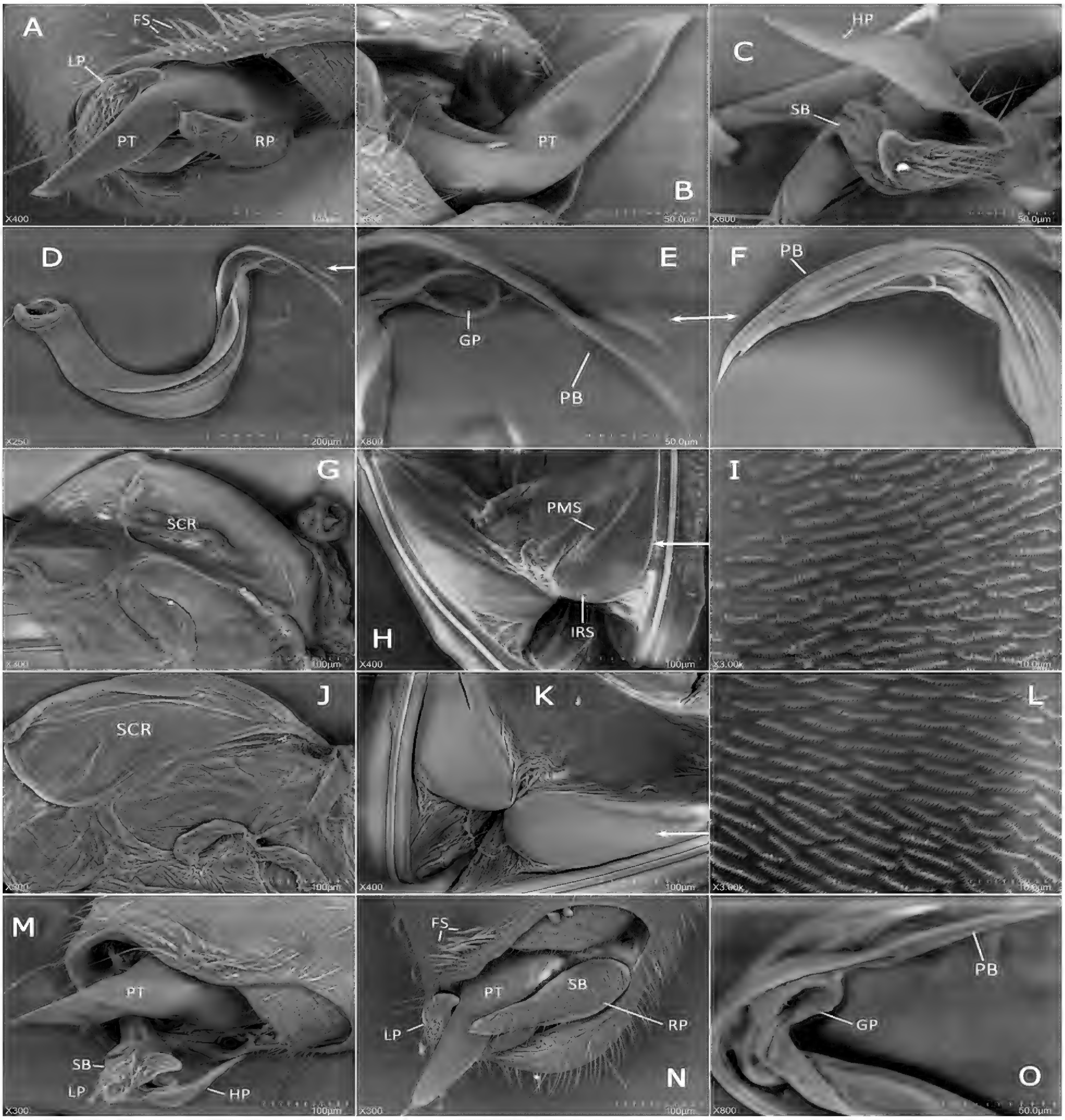

Fig. 9. A–F, M–O. Scanning electron micrographs of ♂ genitalia. **G–L**. Scanning electron micrographs of ♀ genitalia. **A–I**. *Plagiognathus marinoccidens* sp. nov. **J–O**. *P. amurensis*. **A, M–N**. Genital segment (pygophore) with phallotheca and parameres, dorsal view. **B**. Phallotheca. **C**. Left paramere. **D–F, O**. Vesica. **G, J**. Genital chamber, dorsal view. **H–I, K–L**. Posterior wall (I, L for structure of IRS in high magnification). Abbreviations: see Material and methods.

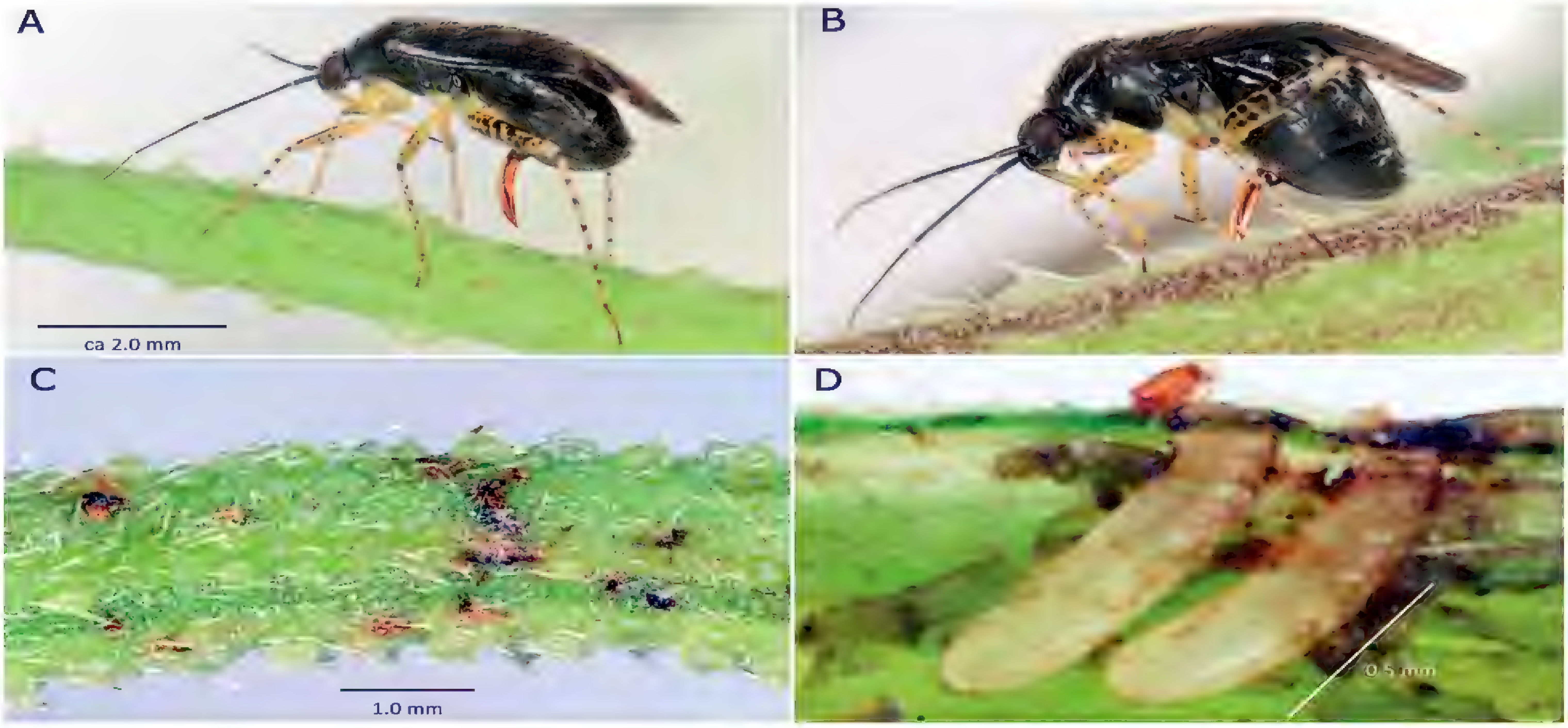

Fig 10. *Plagiognathus marinoccidens* sp. nov. **A–B**. Oviposition behavior. **C**. Brownish pasty coats sealing opercula **D**. Eggs deposited into stem-vine of the Japanese hop.

Schuh (2004) suggested that *Plagiognathus* species were associated with 39 vascular plant families and a number of members were arboreal including conifer-inhabitants. The Japanese species, except for *P. pini* Vinokurov, are known to feed on herbaceous weeds or climbers (see checklist above). So far as I am aware, predaceous food habit is yet to be reported for any Asian *Plagiognathus* species. However, both adults and immature forms of *P. marinoccidens* were recently observed to have positively preyed on an aphid, *Phorodon japonensis* Takahashi, 1965 (Aphididae) which often co-occurs with the plant bug on the Japanese hop, *Humulus japonicus* (Fig. 3H). In addition, the adults and every instar nymphs were successfully reared with a synthetic diet (diluted fermented milk beverage and dried brine shrimp eggs, Fig. 3E–F), and all the immature forms developed into adults. The newly emerged females were observed to oviposit 3–4 days after eclosion (Fig. 10A–B) and to survive for 15–29 days (see the above type material section). When the adults were reared only with the pieces of the host plant, all were dead within a week and the females did not oviposit. Based on available evidences, this new phyline species appears more or less predaceous despite being a specialist of *Humulus japonicus*. Several reared adults were also observed to scavenge on fresh cadavers of small-sized dipteran flies (*Drosophila* sp., *Megaselia* sp. and *Aedes albopictus* as in Fig. 3K). Two aphid species, *Macrosyphoniella sanborni* (Gillette) (original host: *Chrysanthemum* × *morifolium* of Asteraceae) and an undetermined aphid from *Quercus dentata* (Fagaceae), were also preyed upon by the adults of the mirid in laboratory tests. Carnivorous food habit is assumed to be essential for propagation of *P. marinoccidens*.

Details of oviposition behavior were documented for relatively few mirid bugs (Wheeler 2001). The present work confirmed that the eggs of *Plagiognathus marinoccidens* sp. nov. were deposited into the stem-vines of the host plant (Fig. 10D). The opercula were found to be wholly concealed by brownish pasty coats that at first sight seem simply the excrement (Fig. 10C). It was not until I was aware of the opercular seal that I could accurately locate the cryptically deposited eggs. However, it is currently not certain which organ (mouth, ovipositor or anus) secretes the brown matter during oviposition. The coating is considered significant for the eggs to survive for more than 7 months, since the aerial parts, or annual vines of the perennial host plant wither up in winter.

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Research article

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Studies of the taxonomy of the *Gekko vittatus* Houttuyn, 1782 complex (Squamata: Gekkonidae):
II. Remarks on the nomenclature and synonymy of the Striped Gecko, *Gekko* (*Lomatodactylus*) *vittatus* Houttuyn, 1782

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Abstract. In the second part of our work on the taxonomy of the *Gekko vittatus* complex we are dealing with the nomenclature and synonymy of *G. vittatus* Houttuyn, 1782. In particular, two available names are discussed and evaluated: *Lacerta ypsilon* Linck, 1783, and *Lacerta zeulonica* Nau, 1791. Both names which were formerly overlooked in the taxonomic literature, proved to be junior synonyms of *G. vittatus* Houttuyn, 1782.

Key words. *Gekko vittatus*; synonyms; taxonomy.

INTRODUCTION

Gekko Vittaus Houttuyn, 1782 [sic], described by the Dutch physician and naturalist Maarten Willem Houttuyn (1720–1798) belongs to the few new descriptions of geckos (nine in total) which were still described in the 18th century, following the three species described by Linnaeus (1758) in the tenth edition of his „Systema Naturae“ (Uetz et al. 2020). It is the oldest name of any gecko which is unchanged and still valid today in its original combination.

A varied, changeful nomenclature with numerous synonyms is characteristic for many early descriptions of herpetological taxa. This is also true for the gecko dealt with in here, *Gekko vittatus*, which has been described several times under various names, from the end of the 18th to the beginning of the 19th century.

In the following we shall deal with two of these old and forgotten names of the Striped gecko (*Gekko* [*Lomatodactylus*] *vittatus* Houttuyn, 1782) and discuss their current taxonomic status.

HISTORY

The generic nomen *Lomatodactylus* was erected by van der Hoeven (1833) who assigned as synonyms of this name the nomina *Gecko* [sic] Houttuyn and Daud[in] as well as *Stellio* Schn[eider] and *Ascalabotes* Cu[vier]. He divided *Lomatodactylus* in several subgenera and placed his *L. vittatus* (sensu *Gekko vittatus*) in the subgenus *Platydactylus* Cuvier, 1816. As synonyms of the latter species he cited by name *Lac[erta] vittata* Gm[elin] and *Stellio bifurcifer* Schn[eider] and referred additionally to figures of this species in Nau (1791) and Bechstein (1800). However, without referring to the partly differing binominal combinations (see below). Not understandable is why van der Hoeven (1833) initially ignored Linnaeus‘ (1758) *Lacerta gecko* but recognized it much later (van der Hoeven 1855). It was largely ignored that it was not Smith (1935) but already Stejneger (1907) who synonymized *Lomatodactylus* (type species *L*[*omatodactylus*] *vittatus*) from van der Hoeven's (1883) paper with *Gekko* (see Wermuth 1965; Bauer 1994).

According to Wood et al. (2020), *Gekko vittatus* Houttuyn, 1782 is the type species of the subgenus *Lomatodactylus* van der Hoeven, 1833 within the genus *Gekko* Laurenti, 1768. Together with *Gekko* (*Lomatodactylus*) *browni* (formerly *Luperosaurus browni* Russell, 1979) and *Gekko* (*Lomatosaurus*) *iskandari* (formerly *Luperosaurus iskandari* Brown, Supriatna & Ota, 2000), *Gekko vittatus* is forming a subclade within the subgenus *Lomatodactylus*. According to the molecular data published by

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Mulcahy et al. (2022), also *Gekko remotus* Rösler, Ineich, Wilms & Böhme, 2012 can be assigned to this subclade.

RESULTS

Taxonomy

The most complete taxonomic overview of *Gekko vittatus* Houttuyn, 1782 was provided by Bauer (1994). His list, which summarized all published names until 1991, contains more than 120 synonyms and chresonyms of this species, including the belonging bibliographic data. Within geckos, the species name *vittatus* (not *Gonatodes vittatus* [Lichtenstein & von Martens, 1856], not *Diplodactylus vittatus* Gray, 1832, not *Hemidactylus vittatus* Gray, 1845 = *Hemidactylus frenatus* Duméril & Bibron, 1836) has been used in various generic combinations: *Lacerta* Linnaeus, 1758, *Gekko* Laurenti, 1768, *Stellio* Schneider, 1792, *Gecko* Brongniart, 1800, *Platydactylus* Cuvier, 1820, and *Lomatodactylus* van der Hoeven, 1833 (see Bauer, 1994).

The original description and figure of *Gekko vittatus* by Houttuyn (1782: 325, Fig. 2) is followed by *Lacerta unistriata* Shaw (1792: unpaginated, Plate 89) (synonym fide Daudin 1802: 136), as the earliest synonym according to the chronological list compiled by Bauer (1994). In the same year Schneider (1792: 22) published the name *bifurcifer,* which he introduced as a substitute name for *Gekko vittatus* (synonymy fide Meyer 1795: 31). For both taxa, no type material is known. Subsequently, Duméril & Bibron (1836: 334) described *Platydactylus bivittatus* with the type locality „Nouvelle Guinée, l'autre de l'ile Waigiou" (syntypes MNHN 2285 and 6714, synonymy fide Loveridge 1948). The latest synonym of *Gekko vittatus* is *Gecko trachylaemus*, described by Peters (1873: 774), type locality „Nord-Australien", holotype ZMB 7511, synonymy fide Peters & Doria (1878).

Gecko vittatus Houttuyn, 1782 is, after *Gekko gecko* (Linnaeus, 1758), the second oldest species of the genus *Gekko* Laurenti, 1768. Two more taxa are still belonging to *G. vittatus* in the context of names introduced after Linnaeus (1758):

Lacerta ypsilon Linck, 1783

The diagnosis of this nomen is limited to one single sentence: „Die mit einem Ypsilon vom Kopf über den ganzen Körper gezeichnete Eidechse" (= the lizard with an ypsilon running from the head along its whole body)

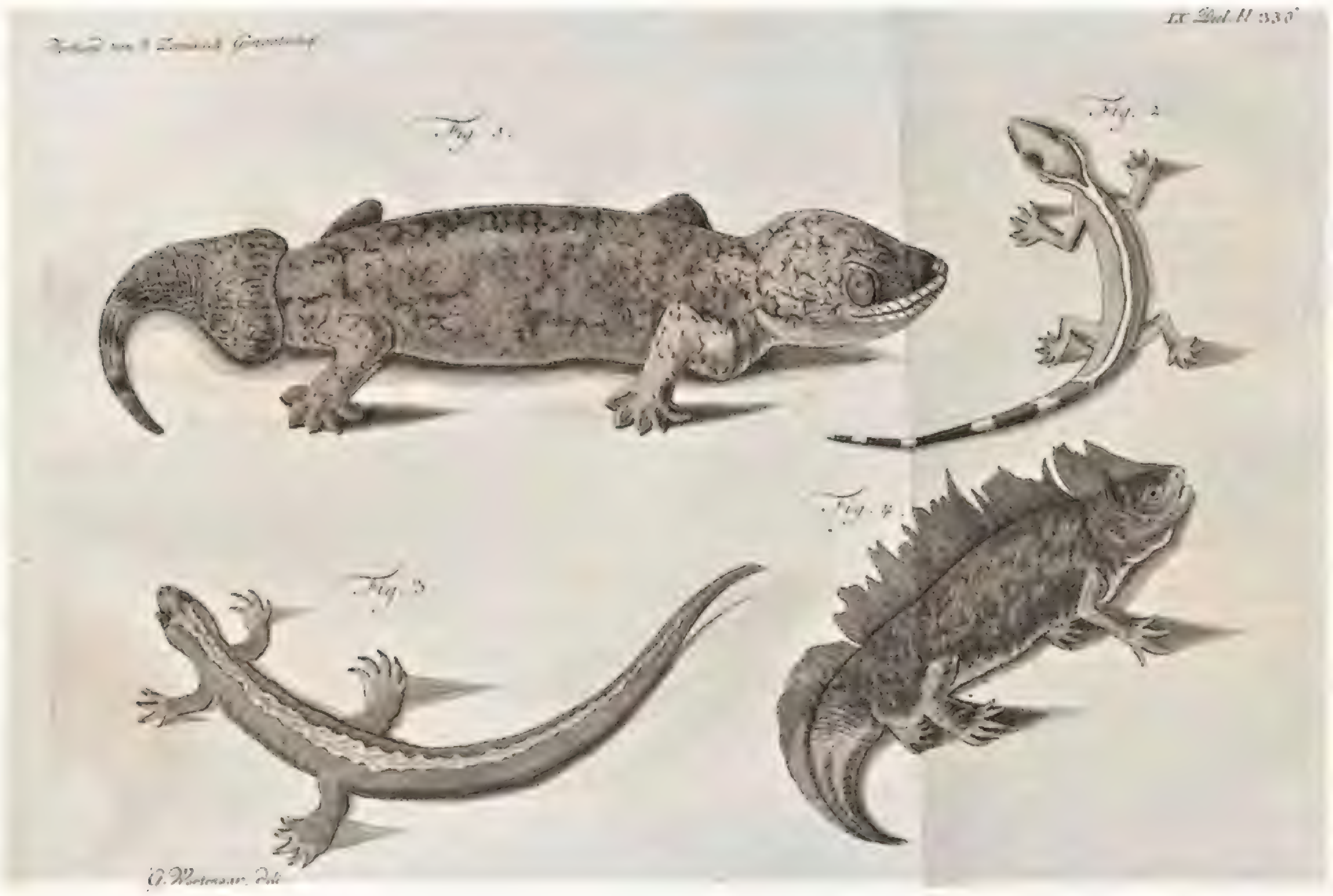

Fig. 1. Plate 9 in Houttuyn (1782). Explanations: Fig. 1. *Gekko Rapicauda* (= *Thecadactylus rapicauda* [Houttuyn, 1782]), Fig. 2. *Gekko Vittatus* (= *Gekko vittatus* Houttuyn, 1782), Fig. 3. *Salamandra Japonica* (= *Onychodactylus japonicus* [Houttuyn, 1782]), Fig. 4. *Salamandra Cristata* (= *Triturus cristatus* [Laurenti, 1768]).

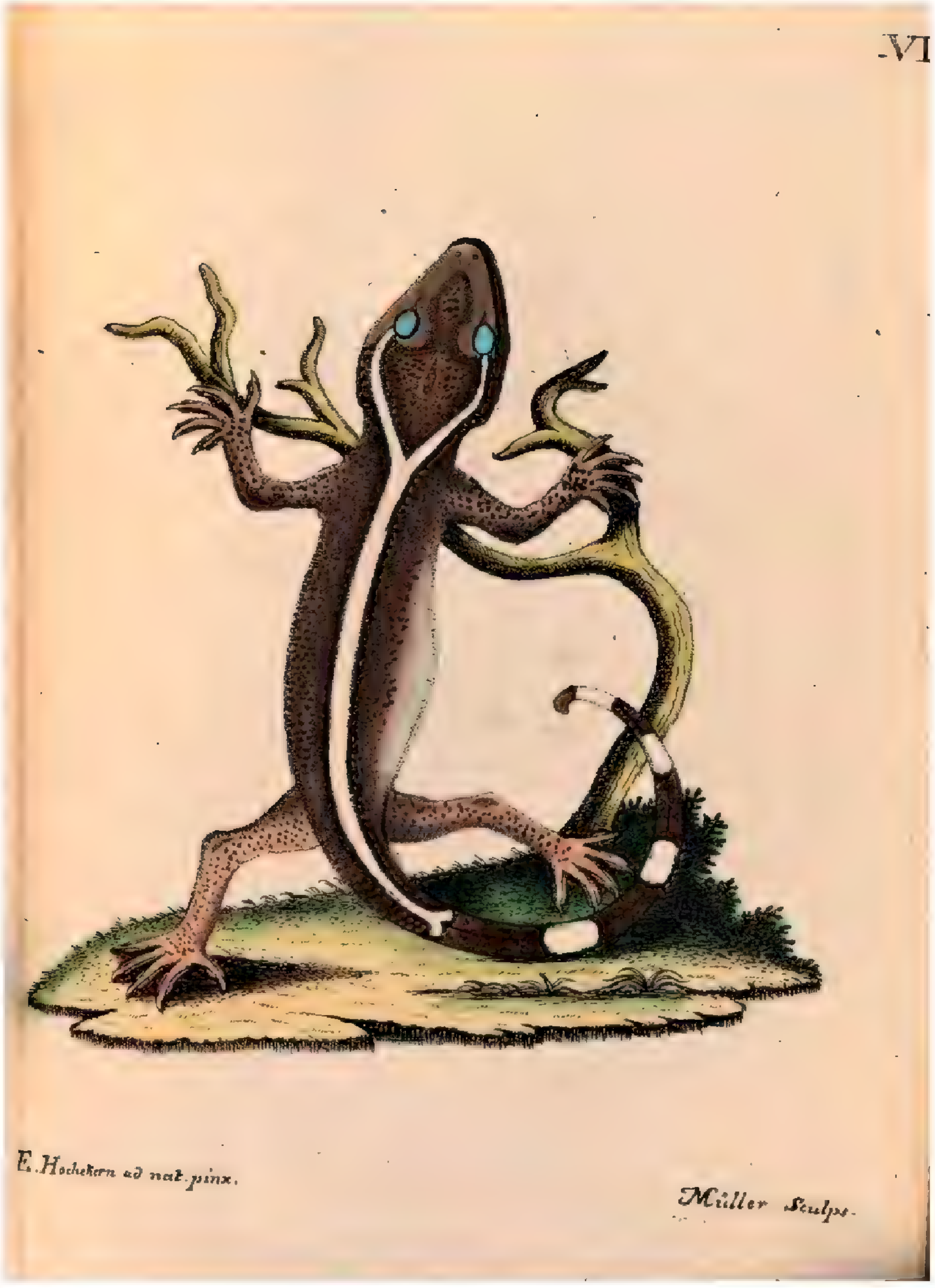
VI
E. Hochstern ad nat. pinx.
Müller Sculps.

Fig. 2. Plate 6 in Nau (1791) with the iconotype of *Lacerta zeulonica* (= *Gekko vittatus* Houttuyn, 1782).

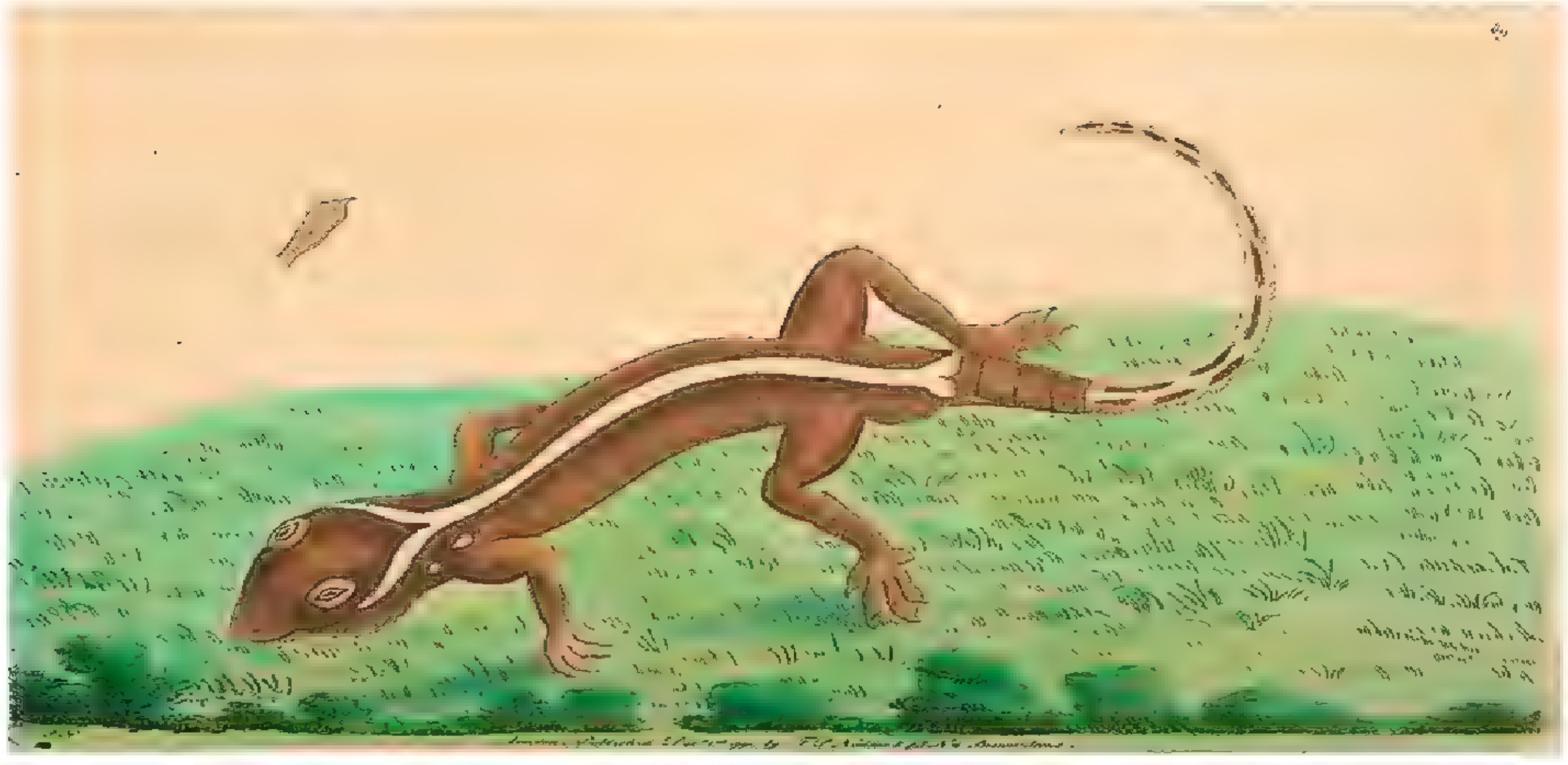

Fig. 3. Plate 89 in Shaw (1792) with *Lacerta unistriata* (= *Gekko vittatus* Houttuyn, 1782).

(Linck 1783: 68). The author was the pharmacist Johann Heinrich Linck the Younger (1734–1807) (Bauer & Wahlgren 2003; Böhme 2015; Engelmann 2018). Linck (1783) identified the herpetological items and arranged them according to the descriptions and figures in Seba (1734, 1735), Scheuchzer (1735), Linnaeus (1766) and of the latter author also according to the German translation by Müller (1774). Because Linck the Younger has always carried out conscientious research (in respect to exact name citations, distribution data, bibliographic hints), it is likely that he was unaware of Houttyun's paper with the description of *Gekko vittatus*. It is not known how the single specimen of *Lacerta ypsilon* had entered the collection. It is possible that it was present already in the collection of his (homonymous) father, Johann Heinrich Linck the Elder (1674–1734), but it is mentioned neither in the cursorily compiled list of his natural history cabinet nor by any other hint (Neickelio 1727).

Schneider (1792), after his intensive research on *Gekko vittatus* Houttuyn, 1782, coined a new name for species, viz. *Stellio bifurcifer* referring to the dorsal pattern (*bifurcifer* from Latin *furca* = fork, *-fer* from *ferre* = to bear, thus bearer of a double fork). He, as the first revisor of this species, criticized that Houttuyn (1782) did not mention the earlier description by Valentyn (1726) under the name „De Pandang hagedis". In addition, he referred to Boddaert (1783) and Gevers (1787), where the same species (sensu Houttuyn 1782) was cited as „Salamandra Pandang" and „Lacerta Pandang" respectively. Notwithstanding the parsimonious data found in Linck's (1783) diagnosis of *Lacerta ypsilon*, Schneider (1792) recognized, obviously based on Linck's figure, that *Gekko vittatus* Houttuyn, 1782 and *Lacerta ypsilon* Linck, 1783 are conspecific. Therefore he synonymized the latter under the name „*lacerta Ypsilon*" [sic] with *Stellio bifurcifer* Schneider, 1792.

In his second monograph on geckos (= *Stellio*), Schneider (1812) complemented his former literature sources on the synonymy of *Stellio bifurcifer* with reference on the publications of Shaw (1792), Bechstein (1800) and Daudin (1802). He mentioned that the paper by Brongniart (1800) was unavailable for him but did not refer to the work by Latreille (1801/1802) although this was cited by Daudin (1802). Likewise, unmentioned by him remained the work by Donndorf (1798) which would have been important here because of its voluminous synonymy list for *Lacerta vittata*.

The synonymization of *Lacerta ypsilon* with *Stellio bifurcifer* by Schneider (1792) is accepted and followed by, e.g., Donndorf (1798) and Bechstein (1800) under the genus name *Lacerta*, and by Tilesius von Tilenau (1817) under *Stellio*. *Lacerta ypsilon* as a junior synonym of *Gekko vittatus* has, however, been left unrecognized by numerous later authors (e.g., Gmelin 1798; Suckow 1798; Daudin 1802; Merrem 1820; Gray 1831; Duméril & Bibron 1836; Fitzinger 1843; Boulenger 1885; Werner 1900; Wermuth 1965; Kluge 1991 and 1993; Bauer 1994; Rösler et al. 2012).

Sherborn's (1932) list does not include the names *Gekko vittatus* and *Lacerta ypsilon*, and he was wrong with the allocation of *Triton vittatus* Guérin-Ménéville, 1838 (= *Ommatotriton vittatus* [Gray, 1835] to the reptiles and not to the urodelan amphibians. Bauer & Wahlgren (2003) cited the name *Lacerta ypsilon* repeating Linck's (1783) list of his natural history collection items, but without referring to its actual status. The last author

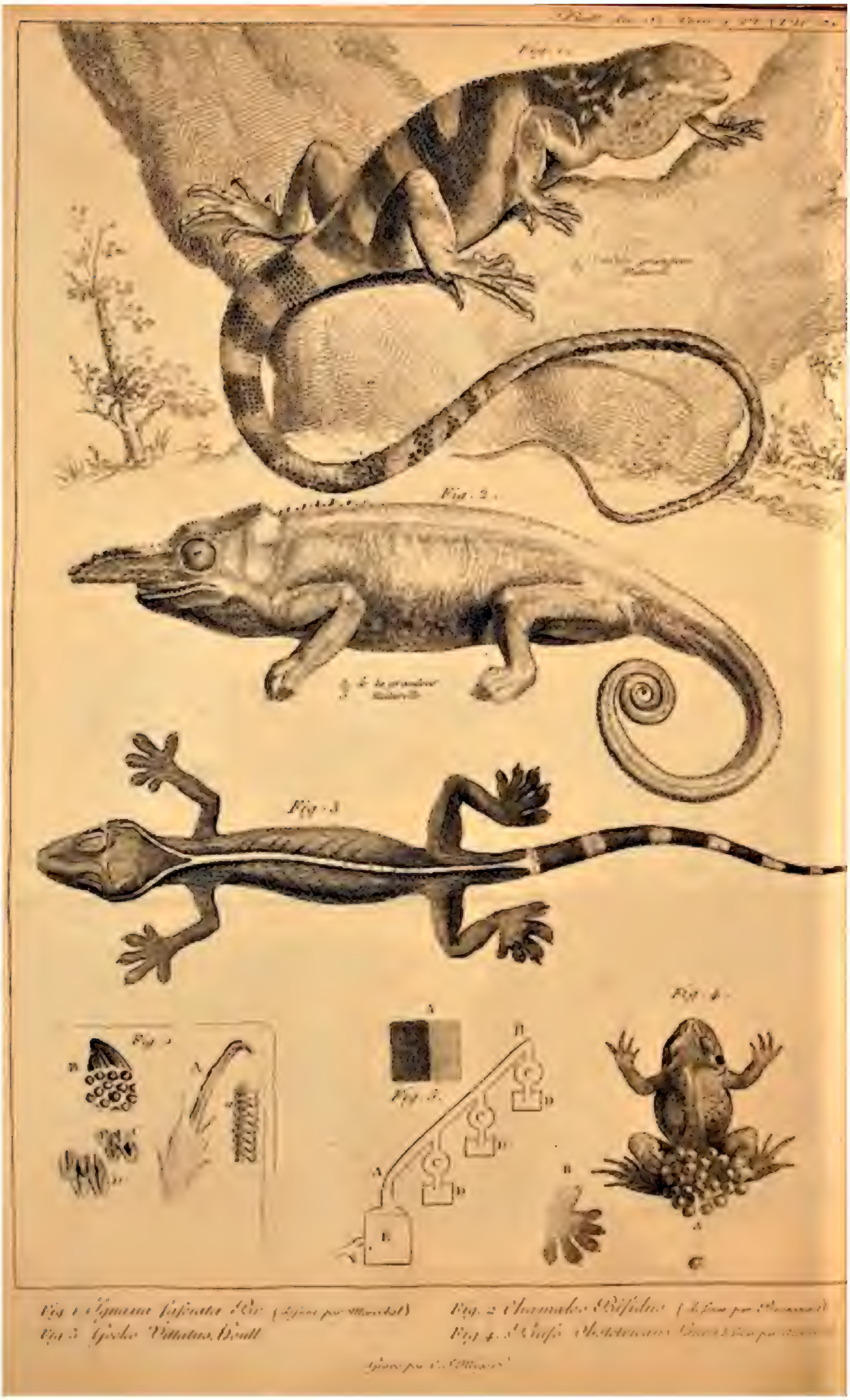

Fig. 4. Plate 6 in Brongniart (1800). Explanations: Fig. 1. *Iguana fasciata* (= *Brachylophus fasciatus* [Brongniart, 1800]), Fig. 2. *Chamaeleo Bifidus* (= *Furcifer bifidus* [Brongniart, 1800]), Fig. 3. *Gecko Vittatus* (= *Gekko vittatus* Houttuyn, 1782), Fig. 4. *Bufo Obstetricans* (= *Alytes obstetricans* [Laurenti, 1768]).

pointing on the synonymy of *Lacerta ypsilon* with *Gekko vittatus* is Engelmann (2018).

Lacerta zeulonica Nau, 1791

Bernhard Sebastian von Nau (1766–1845) was a German naturalist (Rösler & Böhme 2022) and is (1791: 245) the author of *Lacerta zeulonica* (see the review by Beckmann 1791). He published the description and the illustration of this gecko assuming that it was a new species, one year earlier than Shaw's (1792) *Lacerta unstriata*. Shaw (1792) pointed out that there was no counterpart of his lizard to be found which he termed with the vernacular name „single-stripes lizard", neither in Seba (1734, 1735) nor in Linnaeus (1758). Shaw (1792) considered (with a question mark) „? *Lacerta vittata* Gmelin, 1789" as a possible synonym of his *L. unistriata* but ignored the source cited by Gmelin (1789) "Houttuyn act. Vlissing. 9. P. 325. t. 2".

In nomenclatural deviation from his former opinion, Shaw published (1802) a second description of the same species, this time under the name *Lacerta Vittata* [sic], adding the vernacular name „white-striped gecko". In the accompanying synonymy list, he cited earlier names and data from Houttuyn (1782), Gmelin (1789) and Schneider (1792), but not from Nau (1791). Remarkably, he omitted also his own earlier description of *Lacerta unistriata* Shaw, 1792 completely.

Schneider (1792) when describing *Stellio bifurcifer*, commented briefly on the original descriptions of *Gekko vittatus* und *Lacerta vittata* Gmelin, 1789. In more detail he dealt with Nau's (1791) species description, but emended unjustifiably Nau's name to „*Lacertae Zeylonicae*" (plural of *Lacerta zeulonica*).

Early illustrations of *Gekko vittatus* Houttuyn, 1782

Pictorially, body shape and external characters of *Gekko vittatus*, partly including also its synonyms, are relatively well documented. Houttuyn (1782) provided together with his species description also an adequate drawing where the typical dorsal pattern is well recognizable (Fig. 1). The first color illustration was published by Nau (1791), simultaneously with his *Lacerta zeulonica* (Fig. 2). One year later, Shaw (1792) provided the second colored illustration of his *Lacerta unistriata*. The gecko figured by him has a partly regenerated tail, whereas all other figures of *Gekko vittatus* documented and discussed here are based on specimens with original, complete tails. Unicolored images of *Gekko vittatus* are found in the works of Brongniart (1800, 1806), Bechstein (1800), Latreille (1801/02), Daudin (1802) and Reichenbach (1892). They differ from each other remarkably in respect to their quality (Figs 4–7, 9, 11). It is obvious, for instance, that the configuration of the toes shows marked differences, particularly the missing claws at the inner toes remained unrecognized when the print templates had

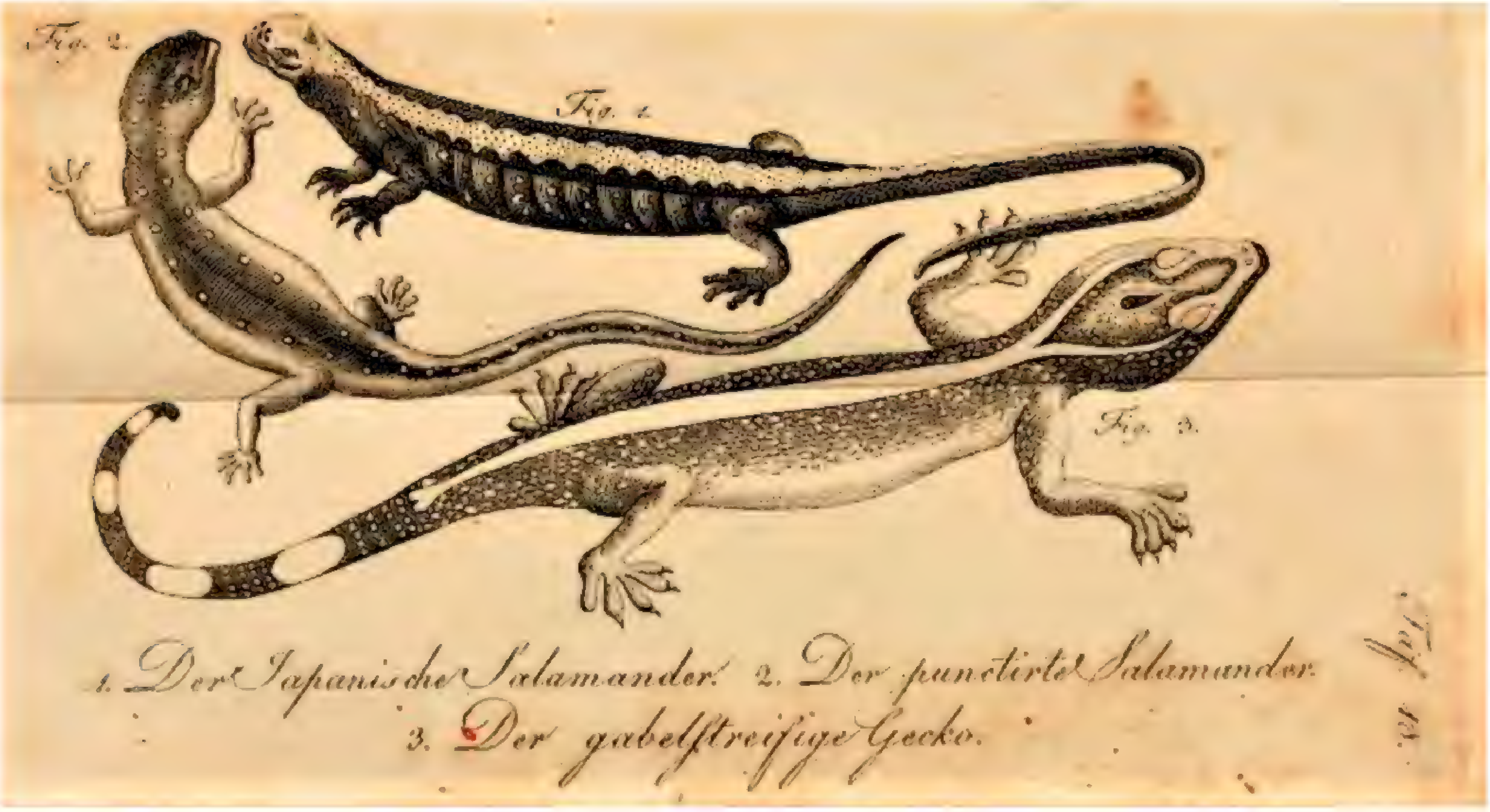
Fig. 2.
Fig. 1.
Fig. 3.
1. Der Japanische Salamander. 2. Der punctirte Salamander.
3. Der gabelstreifige Gecko.

Fig. 5. Plate 18 in Bechstein (1800). Explanations: Fig. 1. Der Japanische Salamander (= *Onychodactylus japonicus* [Houttuyn, 1782]), Fig. 2. Der punctierte Salamander (*Lacerta punctata* Linnaeus, 1766 = *Ambystoma maculatum* [Shaw, 1802], non *Lacerta punctata* Linnaeus, 1758 = *Riopa punctata* [Linnaeus, 1758], fide Bauer 2003), Fig. 3. Der gabelstreifige Gecko (= *Gekko vittatus* Houttuyn, 1782).

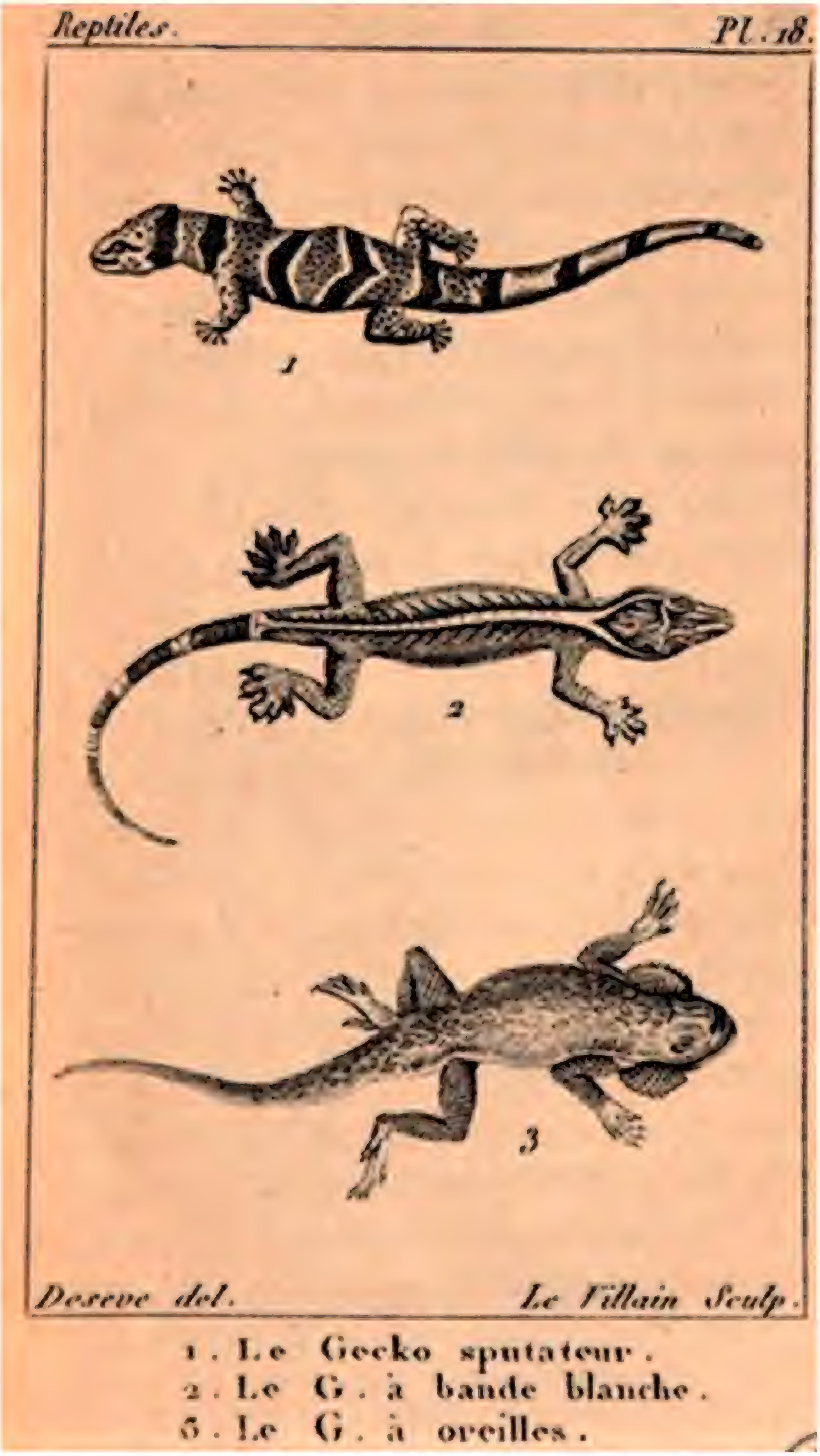
Reptiles.
Pl. 18.
1
2
3
Deseve del.
Le Villain Sculp.
1. Le Gecko sputateur.
2. Le G. à bande blanche.
3. Le G. à oreilles.

Fig. 6. Plate 18 in Lattreille (1801/1802). Explanations: Fig. 1. Le Gecko sputateur (= *Sphaerodactylus sputator* [Sparrman, 1784], Fig. 2. Le G[ecko] à bande blanche (= *Gekko vittatus* Houttuyn, 1782), Fig. 3. Le G[ecko] oreilles (= *Phrynocephalus mystaceus* [Pallas, 1776]).

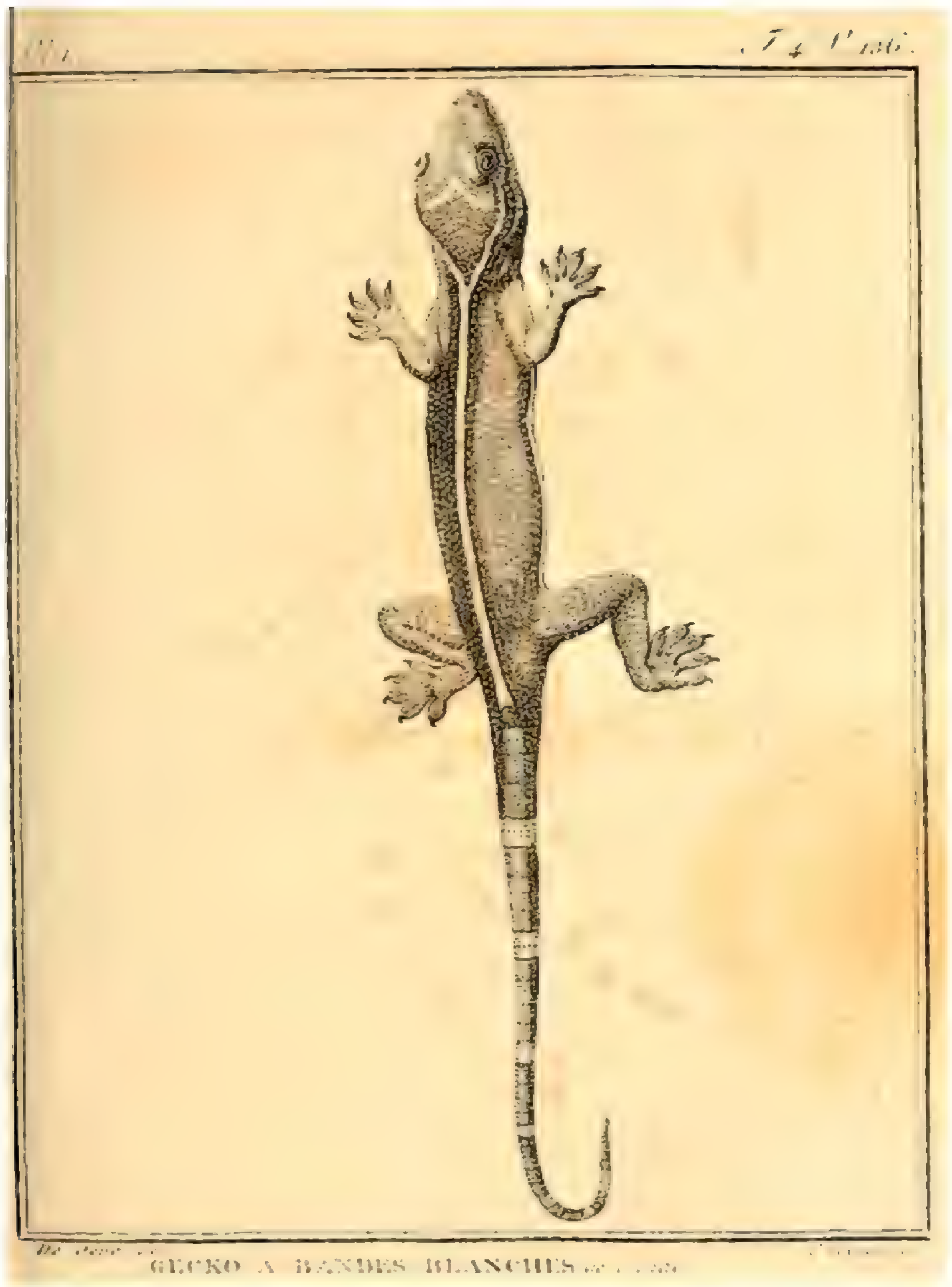

Fig. 7. Plate 50 in Daudin (1802) with Gecko à bandes blanches (= *Gekko vittatus* Houttuyn, 1782).

been prepared. The figures in Bechstein (1800) and Reichenbach (1829) were most likely inspired by the color plate in Nau (1791). Just as in this plate, the tail pattern is figured with the same number of white, oval-shaped flecks, rather than with the sharply limited crossbands as in the other figures. Strack (1820) copied off the portraits of three urodelans and of the gecko from plate 14 in Bechstein (1800), but the combination of colors of different body parts (upperside bluish, underside yellowish white) in this hand-colored plate is incorrect (Fig. 10). Illustrations with a high level of exactness in respect of the diagnostic characters of *Gekko vittatus* are those by Oppel (see Rösler & Schmidtler 2014) and by Duvernoy (1839) (Figs 8 and 12).

All illustrations presented here show the typical morph of *Gekko vittatus* which is characterized by a white dorsal stripe which bifurcates in the nape, both branches extending to the hind margin of the eyes. A stylized picture series of phenotypically differing *G. vittatus*-forms, which were mentioned already in word and picture by Werner (1900), Mertens (1934), McCoy (2006), and Rösler et al. (2012), has been compiled by Grossmann & Kreuzer (2012).

Distribution

The distribution center of *Gekko vittatus* is New Guinea. Other populations are known from numerous Indo-Australian islands (Lesson 1830 a, b; Werner 1900; de Rooij 1913 and 1915; Sternfeld 1920).

Based on the place of origin „zekerlyk uit de Indiën“ in Houttuyn (1782), Gmelin (1789) gave „India“ as the type locality of *G. vittatus*. However, an occurrence of this species in India has neither temporarily nor permanently been recorded (Günther 1864; Boulenger 1890; Smith 1935; Sharma 2002; Das 2003; Aengals et al. 2018). The earliest verifiable statement for the correct distribution range of *G. vittatus* is to be found in Valentyn (1726). According to his data this gecko is present in Amboina (= Ambon, Moluccas, Indonesia), but is found rarely on „Strand Padang“ plants (*Cinnamomum* sp.). It is very likely that that Houttuyn's specimen reached Europe from the Moluccas on one of the „Netherland's East Indian Company“ sailing ships involved in the most profitable spice trade.

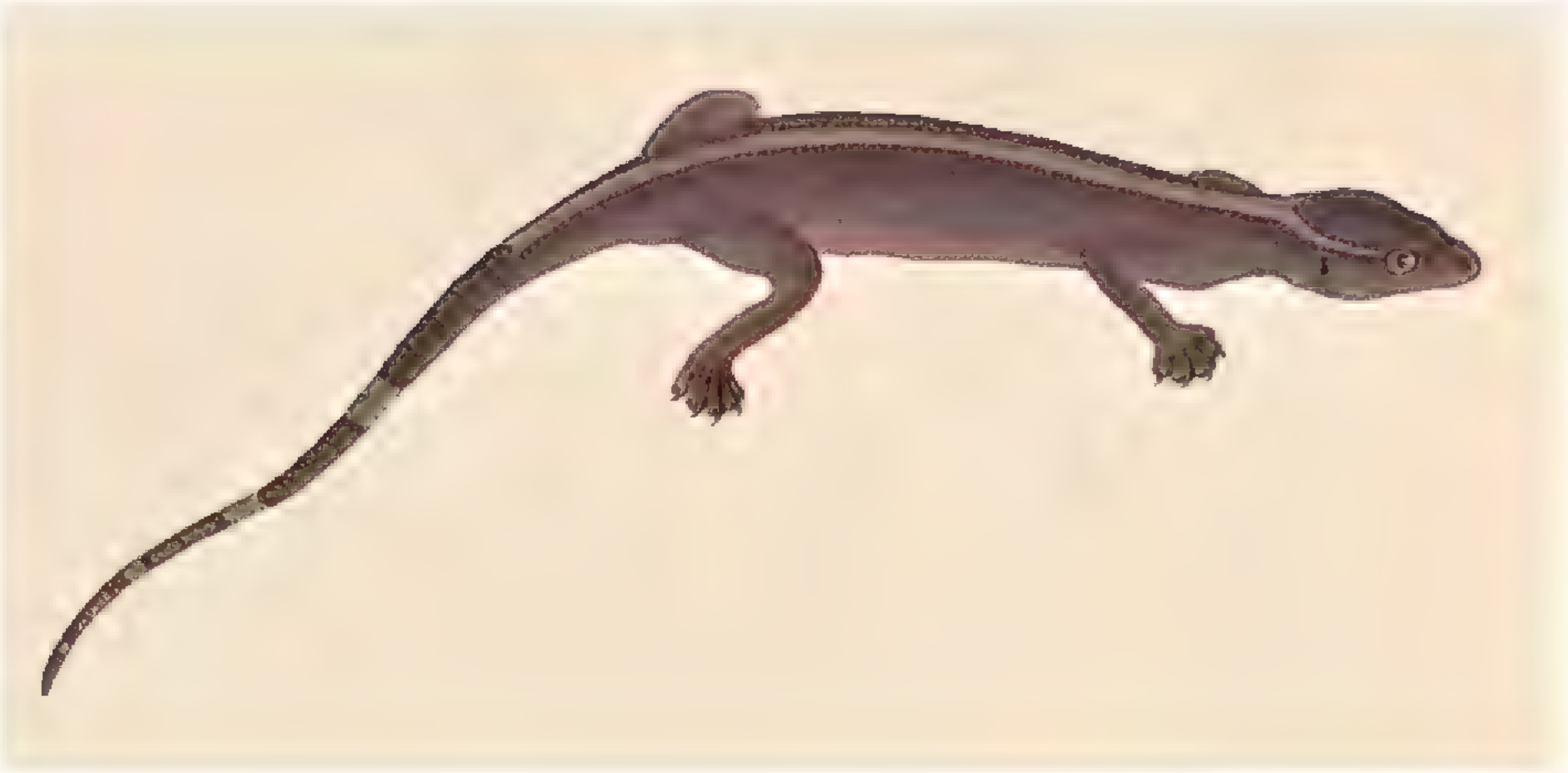

Fig. 8. Watercolor with *Gekko vittatus* Houttuyn, 1782, drawn between 1807–1809 by Nikolaus Michael Oppel from Rösler & Schmidtler (2014).

The place of origin of *Lacerta ypsilon* is unknown. The label inscription (see Fig. 375 in Engelmann 2018) is likely not based on an information by Linck the Younger because he had listed all locality data as far as known to him, most carefully in his „Index Musaei.“ Both geographical hints can likely be deduced from the re-arrangement and re-identification of the zoological subjects by Konstantin Wöpke (1903–1944) where the data have retroactively been added (Seifert 1934; Wöpke 1937). Possibly this was influenced by earlier notes of various taxidermists which were concerned with the curation of Linck's natural history collection between 1849 and 1927 (see Zinke 2015). With missing locality data and based only on its morphological characters, *Lacerta ypsilon* can only be assigned to the nominotypic form of *Gekko vittatus*.

The description of *Lacerta zeulonica* is based on a specimen which Nau has likely received from the Dutch naturalist Arnout Vosmaer (1720–1799) who was a fanatic collector of zoological items (Adler 2012). The lat-

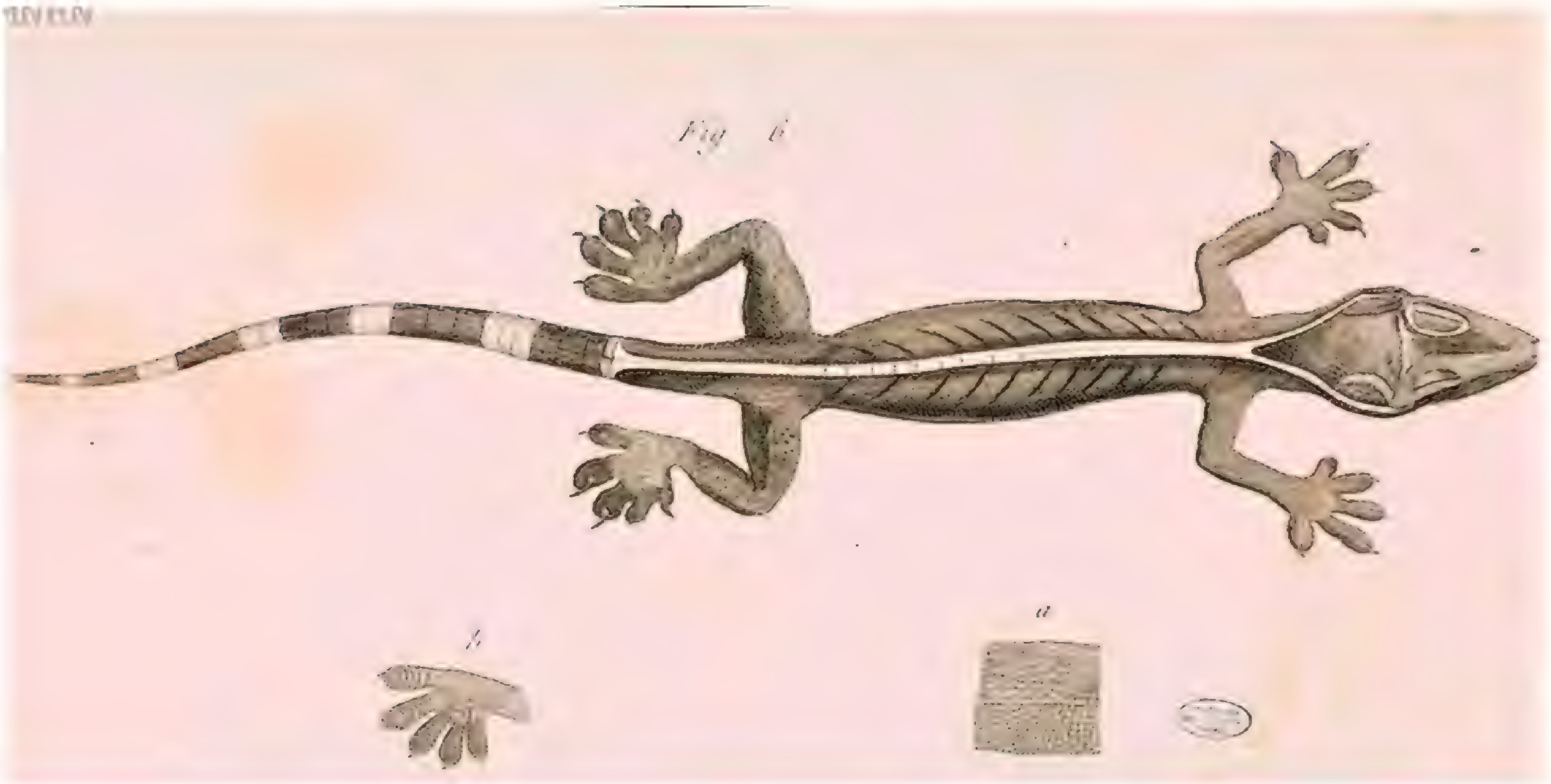

Fig. 9. Plate II, Figur 6: Gecko rayé, *G. vittatus* (= *Gekko vittatus* Houttuyn, 1782) in Brongniart (1806: 622). Source: Calames, Muséum national d'histoire naturelle (Paris) – Direction des bibliothèques et de la documentation.

ter (in Nau 1791 spelled „Vosmär") assured him that the specimen originated from „Zeulon" (Ceylon = Sri Lanka). This seemingly precise locality obviously influenced Nau to choose the corresponding geographic epitheton. It cannot be decided here who was lastly responsible for the denomination, since Houttyun and Vosmaer knew each other, and Houttuyn was at least familiar with the description of *Gekko vittatus*. Amarasinghe et al. (2009) did not mention *Lacerta zeulonica* in their treatment of Sri Lankan geckos described in three centuries, and according to Silva (1994), there are no species of the genus *Gekko* occurring on this island. On the other hand, description and figure of *Lacerta zeulonica* leave no doubt for its identity with *Gekko vittatus* so that its true geographic origin lies certainly within the distribution range of *G. vittatus* as outlined by Bauer (1994).

The records of various *Gekko vittatus* populations without the characteristic phenotypic white and anteriorly forked dorsal stripe stem from various archipelagos widely separated from each other. Differences in morphology and color pattern of *G. vittatus* sensu lato have been described by Werner (1900) and Sternfeld (1930). A relatively dark form from Nissan Atoll (Papua New Guinea) was figured by Mertens (1934) with the comment that a dark (melanistic) color phase is known from many Papuan islands. Photographic records of a second, more intensively light/dark marbled form have been published from some Solomon Islands (Malaupaina Id., Olu Malau Ids.) by McCoy (1980 and 2006).

Preliminarily described from Micronesian Palau islands was *Gekko remotus*, a member of the *G. vittatus* species complex (Rösler et al. 2012; Mulcahy et al. 2022), but the status of several other geographic island populations deserves further morphological and molecular studies.

Nomenclature

Lacerta ypsilon Linck, 1783 has been published before 1931 and meets therefore the requirements of availability (art. 12 ICZN). The type specimen is deposited in the Natural History Cabinet of the Museum in Waldenburg (catalog number in Linck 1783: 290; Inventory number of the Museum Waldenburg: NAT 2027). The name has to be considered as a junior synonym of *Gekko vittatus* Houttyun, 1782 (sensu stricto), if the conspecifity of both taxa is corroborated. If not, *Lacerta ypsilon* is an available name (ICZN Code, Article 23).

Lacerta zeulonica Nau, 1791, also published before 1931, is likewise a valid, available name. The whereabout of the type material is unknown. Based on the description and figure, its former allocation (see above) as a junior subjective synonym of *Gekko vittatus* Houttuyn is maintained.

Acknowledgements. We thank Sandra Nagy (Museum – Naturalienkabinett Waldenburg) for her research in the old catalogues of the natural history collection under her care. For providing literature references we thank Gabriele Lehmann (Bibliothek Thale), and Ursula Bott (Museum Koenig Bonn) is greatly acknowledged for technical support.

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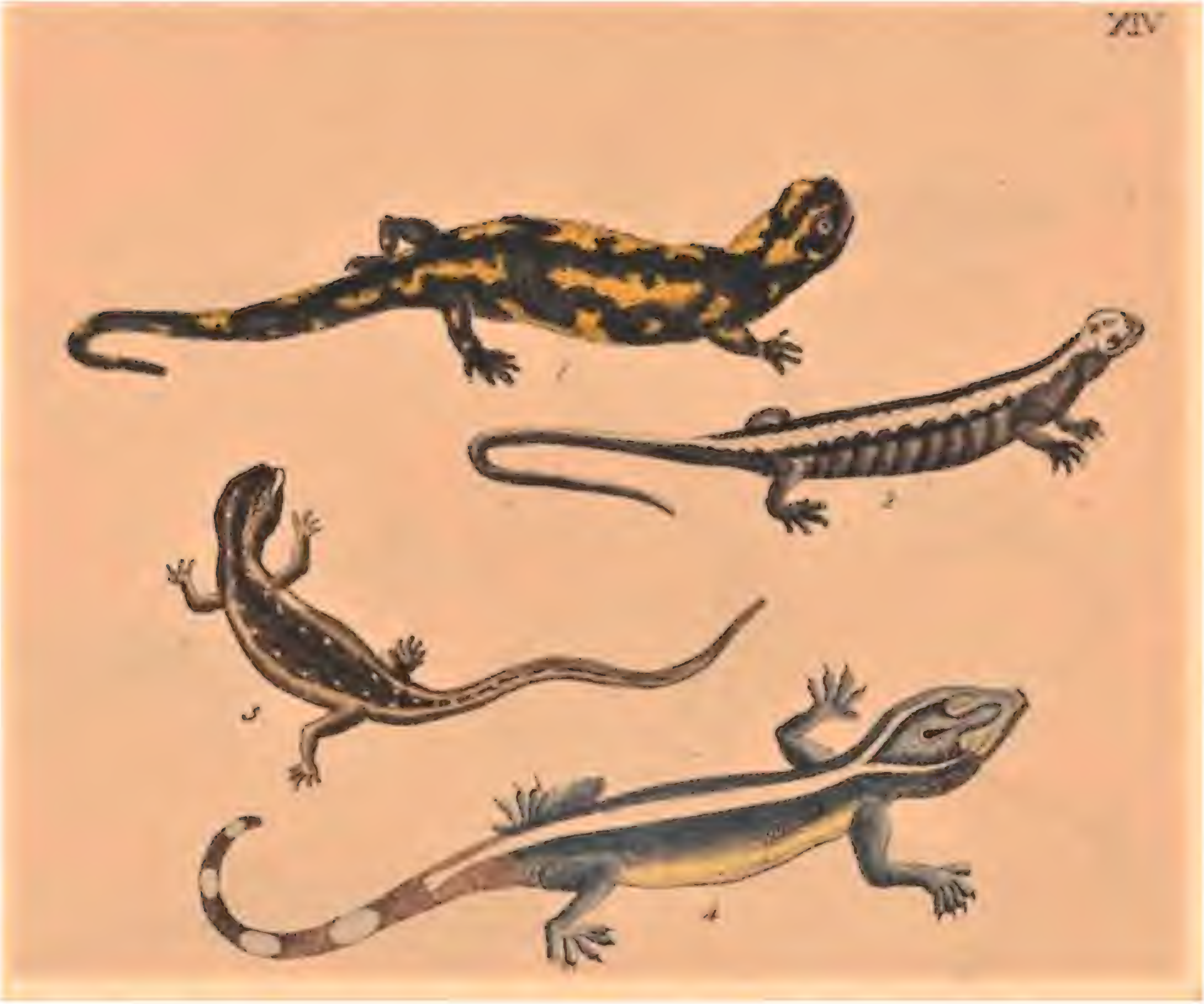

Fig. 10. Plate 14 in Strack (1820). Explanations: Fig. 1. Der gemeine Erdsalamander, *Lacerta salamandra* (= *Salamandra salamandra* [Linnaeus, 1758]), Fig. 2. Der Japanische Salamander, *Lacerta salamandra iaponica* sic (= *Onychodactylus japonicus* [Houttuyn, 1782]), Fig. 3. Der punktierte Salamander, *Lacerta salamandra punctata* (= *Ambystoma maculatum* [Shaw, 1802], cf. Fig. 5), Fig. 4. Der gabelstreifige Gecko, *Lacerta bifurcifer* (= *Gekko vittatus* Houttuyn, 1782).

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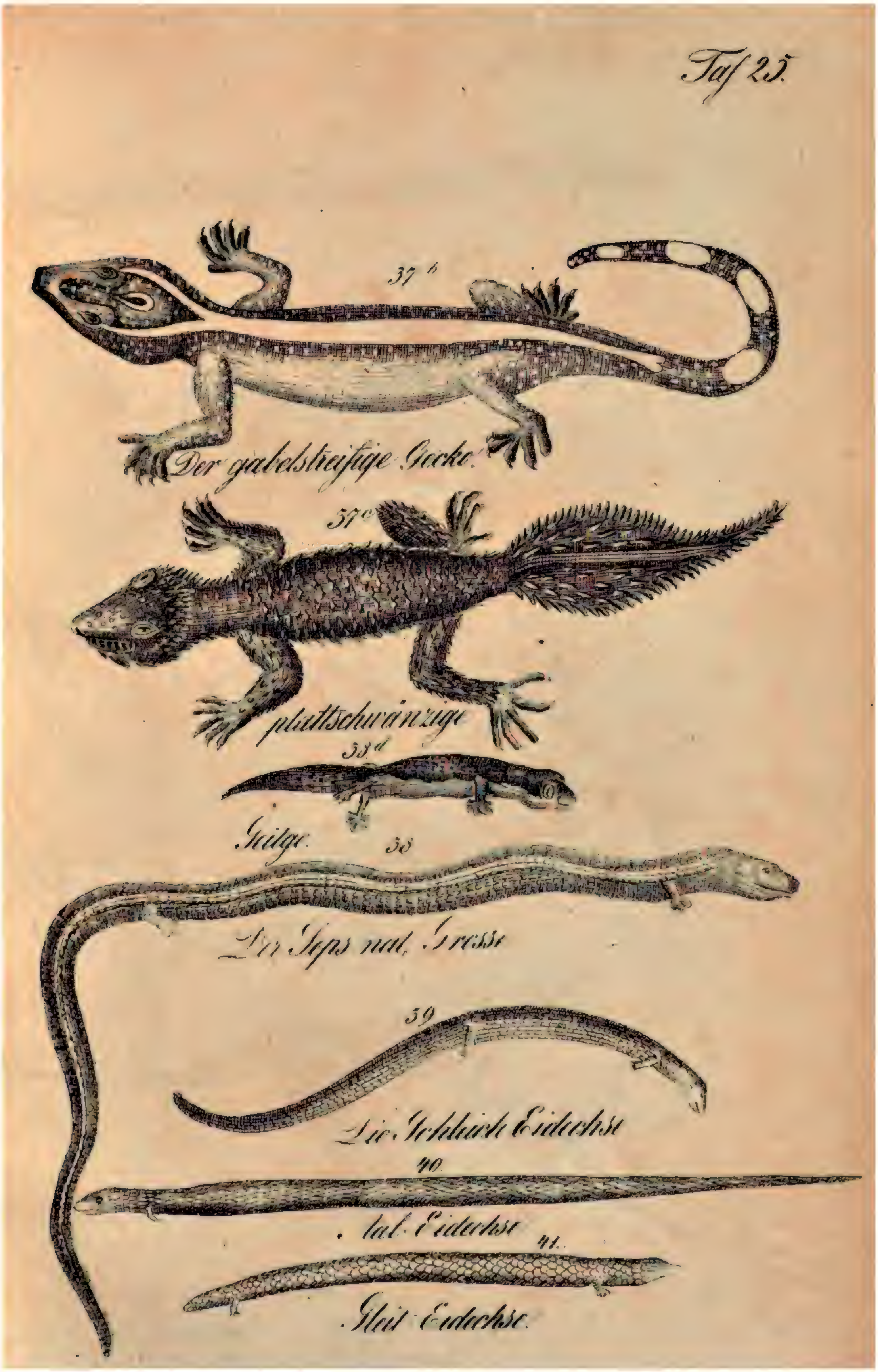

Fig. 11. Plate 25 in Reichenbach (1829). Explanations: Fig. 37b. Der gabelstreifige Gecko (= *Gekko vittatus* Houttuyn, 1782), Fig. 37c. [Der] plattschwänzige [Gecko] (= *Phyllurus platurus* [Shaw, 1790]), Fig. 37d. Geitge (= *Pachydactylus geitje* [Sparrman, 1778]), Fig. 38. Der Seps (= ? *Bachia* sp., non *Lacerta seps* Linnaeus, 1758 = *Tetradactylus seps* [Linnaeus, 1758]), Fig. 39. Die Schleich Eidechse (= *Lygosoma quadrupes* [Linnaeus, 1766]), Fig. 40. Aal Eidechse (= *Chamaesaura anguina* Linnaeus, 1758), Fig. 41. Gleit Eidechse (= ? *Lygosoma quadrupes* [Linnaeus, 1766])

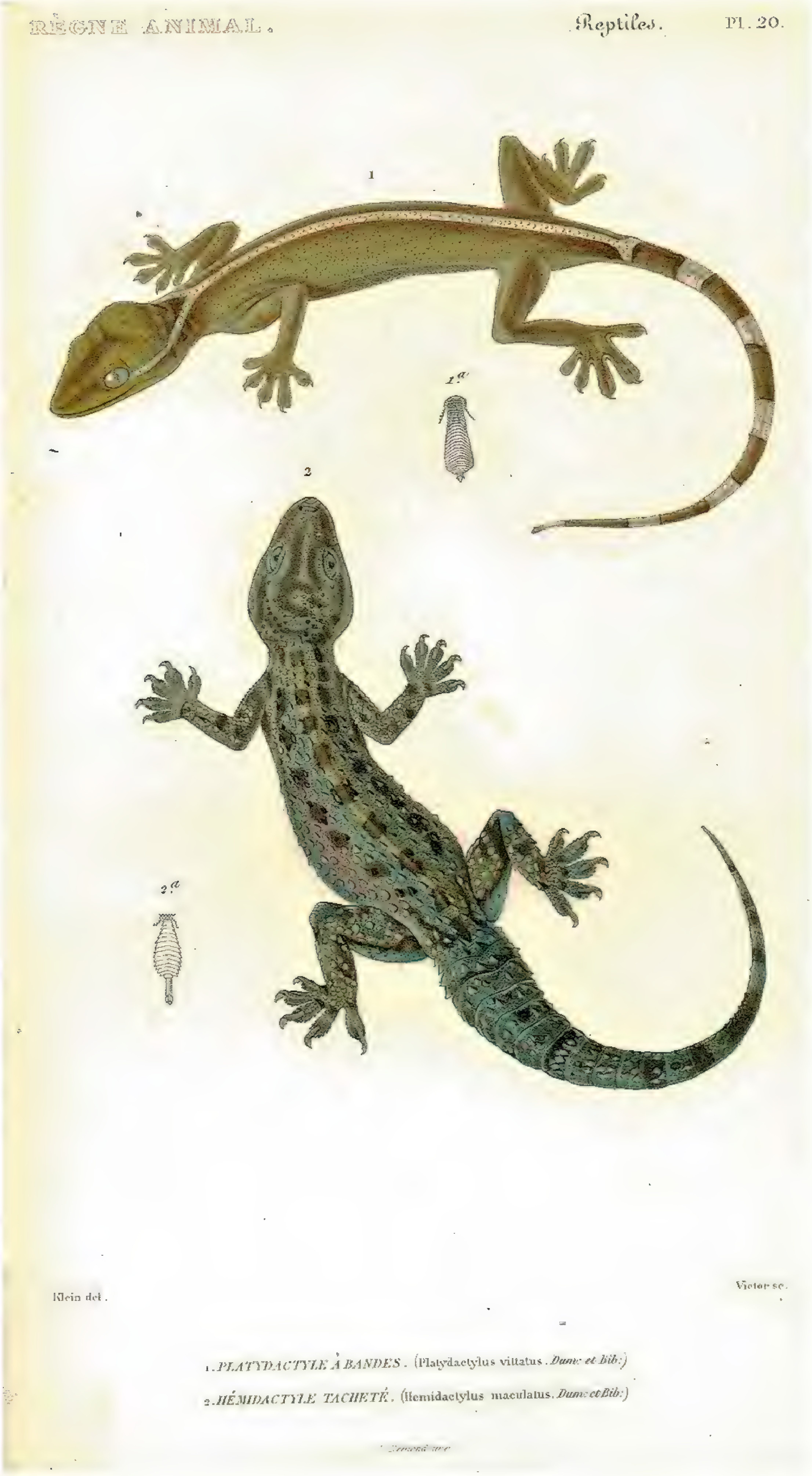
RÈGNE ANIMAL.
Reptiles.
Pl. 20.
1
1.a
2
2.a
Klein del.
Victor sc.
1. PLATYDACTYLE À BANDES. (Platydactylus vittatus. Dum: et Bib:)
2. HÉMIDACTYLE TACHETÉ. (Hemidactylus maculatus. Dum: et Bib:)

Fig. 12. Plate 20 in Duvernoy (1839). Explanations: Fig. 1. Platydactele à Bandes. (*Platydactylus vittatus* Dum: et Bib:) (= *Gekko vittatus* Houttuyn, 1782), Fig. 2. Hémidactyle Tacheté (*Hemidactylus maculatus* Dum: et Bib:) (valid).

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Research article

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Two new species of *Archeohomaloplia* Nikolajev, 1982 from China (Coleoptera: Scarabaeidae: Sericini)

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Abstract. Two new species, *Archeohomaloplia xiajuan* sp. nov. and *Archeohomaloplia volkovitchi* sp. nov., are described and illustrated from Yunnan (China). The key to the species of *Archeohomaloplia* Nikolajev, 1982 is updated and additional new records of the genus are given.

Keywords. Coleoptera; beetles; scarab chafers; Yunnan; China; new species.

INTRODUCTION

This paper is a further update on a comprehensive taxonomic revision of the Sericini of China and adjacent regions. All genera of Sericini occurring in China have been revised at least once, for several groups further updates have been given as well (Ahrens 1996, 2000a, 2000b, 2000c, 2001, 2003a, 2003b, 2003c, 2003d, 2005a, 2005b, 2006a, 2006b, 2006c, 2007a, 2007b, 2007c, 2009, 2011, 2021a, 2021b, 2021c; Ahrens et al. 2014a, 2014b, 2014c, 2021a, 2021b, 2022, in press; Liu et al. 2011, 2014a, 2014b, 2014c, 2014d, 2014e, 2015a, 2016, 2017a, 2017b, 2019; Ahrens & Pacholátko 2003, 2007; Ahrens & Fabrizi 2009a, 2009b, 2011; Bohacz & Ahrens 2020; Fabrizi et al. 2021).

The genus *Archeohomaloplia* Nikolajev, 1982 was originally erected by Nikolajev (1982) mainly based on its differences to the genus *Omaloplia* Schoenherr, 1817, such as the antenna being composed by ten antennomeres (instead of nine) (see Ahrens 2011). Originally, it included only two species (*A. potanini* Nikolajev, 1982 and *A. medvedevi* Nikolajev, 1982), while subsequently a third species of a recently erected genus *Melanomaladera* Miyake & Yamaya, 2001, *M. yunnana* Miyake & Yamaya, 2001, was assigned as well to *Archeohomaloplia* (Ahrens 2007). Ahrens (2007) also synonymized *A. potanini* Nikolajev, 1982 with the senior synonym, *Homaloplia abbreviata* Fairmaire, 1897, and he added later other ten species to the genus (Ahrens 2011). All species are so far known to be endemic to the area between Yunnan and northern Indochina (Myanmar/Thailand). Here, I describe further two new species of the genus *Archeohomaloplia* Nikolajev, 1982, which were discovered among specimens of the ZIN that Andrey Frolov kindly made available for study a couple of years ago.

MATERIAL AND METHODS

The terminology and methods used for measurements, specimen dissection and genital preparation follow Ahrens (2004). Data from specimens examined are cited in the text with original label contents given in quotation marks, multiple labels for a single specimen are separated by a "/". Descriptions and illustrations of new taxa are based on the holotype specimen if not otherwise stated, while the variation of specimens is given separately under "variation". Male genitalia were glued to a small pointed card and photographed in both lateral and dorsal views using a stereomicroscope Leica M125 with a Leica DC420C digital camera. A number of single focussed images were combined with the Automontage software in order to obtain an entirely focussed image. The resulting images were subsequently digitally edited.

Institutional abbreviations

ZFMK = Zoologisches Forschungsmuseum A. Koenig, LIB Bonn (Germany);
ZIN = Zoological Institute, Russian Academy of Sciences, St. Petersburg (Russia).

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RESULTS

Archeohomaloplia xiajuan sp. nov.
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Fig. 1

Type material examined. Holotype: ♂ "Yunnan 70km NNW Xiajuan 24.V.2002 Volkovitch/ Asia Sericini sp 1158" (ZIN).

Description. Length: 4.9 mm, length of elytra: 3.1 mm, width: 2.5 mm. Body oblong, black, antenna black, dorsal surface shiny, with sparse and evenly spaced long, erect setae.

Labroclypeus trapezoidal, widest at base and strongly convergent apically, lateral margins weakly convex; anterior angles almost blunt, only weakly rounded; lateral border and ocular canthus producing an indistinct blunt angle; margins moderately reflexed, anterior margin moderately emarginate medially; surface medially convex and shiny, finely and densely punctate, distance between punctures less than their diameter, with a few robust punctures behind anterior margin bearing each a long, erect seta; frontoclypeal suture feebly incised, distinctly elevated and moderately curved; smooth area in front of eye approximately 1.2 × as wide as long; ocular canthus short and wide, subtriangular, rounded at apex, finely and densely punctate, with one terminal seta. Frons shiny, with fine, dense punctures; with numerous erect setae behind the frontoclypeal suture and beside eyes. Eyes very small, ratio of diameter/interocular width: 0.39. Antenna brown, with ten antennomeres; club dark brown, with three antennomeres, little shorter than remaining antennomeres combined. Mentum weakly elevated and flattened anteriorly.

Pronotum moderately wide, widest at middle, lateral margins strongly curved and slightly convergent basally, but stronger convergent anteriorly; anterior angles strongly produced and sharp, posterior angles strongly rounded and almost obsolete; anterior margin convexly produced medially, with a broad marginal line; basal margin with fine and complete marginal line; surface with dense and fine punctures, with a few long yellow, semierect setae on disc; anterior and lateral borders densely setose; hypomeron simple, not carinate at base and consequently not ventrally produced. Scutellum triangular and dull, slightly longer than wide, with fine and dense punctures, with minute setae in punctures.

Elytra oblong, widest in apical third, striae weakly impressed, finely and densely punctate, intervals weakly convex, with fine, moderately dense punctures often concentrated along the striae, odd intervals with single, fine, long, yellow setae (setae longer than interval width); interior apical angle of elytra with a short seta; epipleural edge fine ending at the strongly curved external apical angle of elytra, epipleura densely setose; apical border of elytra with a narrow membraneous rim of short microtrichomes.

Ventral surface shiny, with fine and moderately dense punctures, finely densely setose; metacoxa glabrous with a few fine, long, adjacent setae laterally only; abdominal sternites micro-reticulate, with an indistinct, transverse row of coarse punctures bearing a moderately long seta between fine, dense punctation, a few fine punctures bear a short seta; penultimate sternite apically with a smooth, sclerotized border which is one fifth as long as the sternite, last sternite medially 0.75 × as long as penultimate one. Mesosternum between mesocoxae as wide as mesofemur, with fine, long setae. Ratio of length of metepisternum/metacoxa: 1/1.48. Pygidium strongly convex at apex, finely and densely punctate, without smooth midline; surface shiny, sparsely covered with short and longer setae.

Legs slender and moderately long; femora shiny, with two longitudinal rows of setae, coarsely but sparsely punctate; metafemur sharply carinate anteriorly and without a submarginal serrate line, posterior margin weakly convex and with a few short setae basally, its ventral part only weakly widened in apical half and not serrate, dorsal posterior margin not serrate, with dense, long setae. Metatibia slender and moderately long, evenly widened towards apex, ratio width/length: 1/3.2; dorsally longitudinally convex, apically also weakly carinate, with two groups of spines, basal group at first quarter, apical group at two thirds of metatibial length, basally with a few single, fine setae; external face longitudinally convex, with fine punctures laterally, glabrous; ventrally with a sharp, finely serrate margin, with four robust setae; internal face laterally with a few punctures bearing each a fine seta; apex interiorly deeply excavate at middle and not truncate near tarsal articulation. Meso- and metatarsomeres dorsally glabrous and finely densely punctate, ventrally with sparse, short setae; metatarsomeres ventrally with a finely serrate ridge, beside it with a robust longitudinal carina; metatarsomere 1 as long as following tarsomere and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetric.

Aedeagus: Fig. 1A–D. Habitus: 1E. Female unknown.

Diagnosis. *Archeohomaloplia xiajuan* sp. nov. is in external appearance rather similar to *A. hebashana* Ahrens, 2011. The new species differs by the shape of the dorsal apophysis of the phallobase which is apically more strongly widened and truncate at apex; the parameres are narrower and weakly curved.

Etymology. The species is named according to its occurrence near Xiajuan (noun in apposition).

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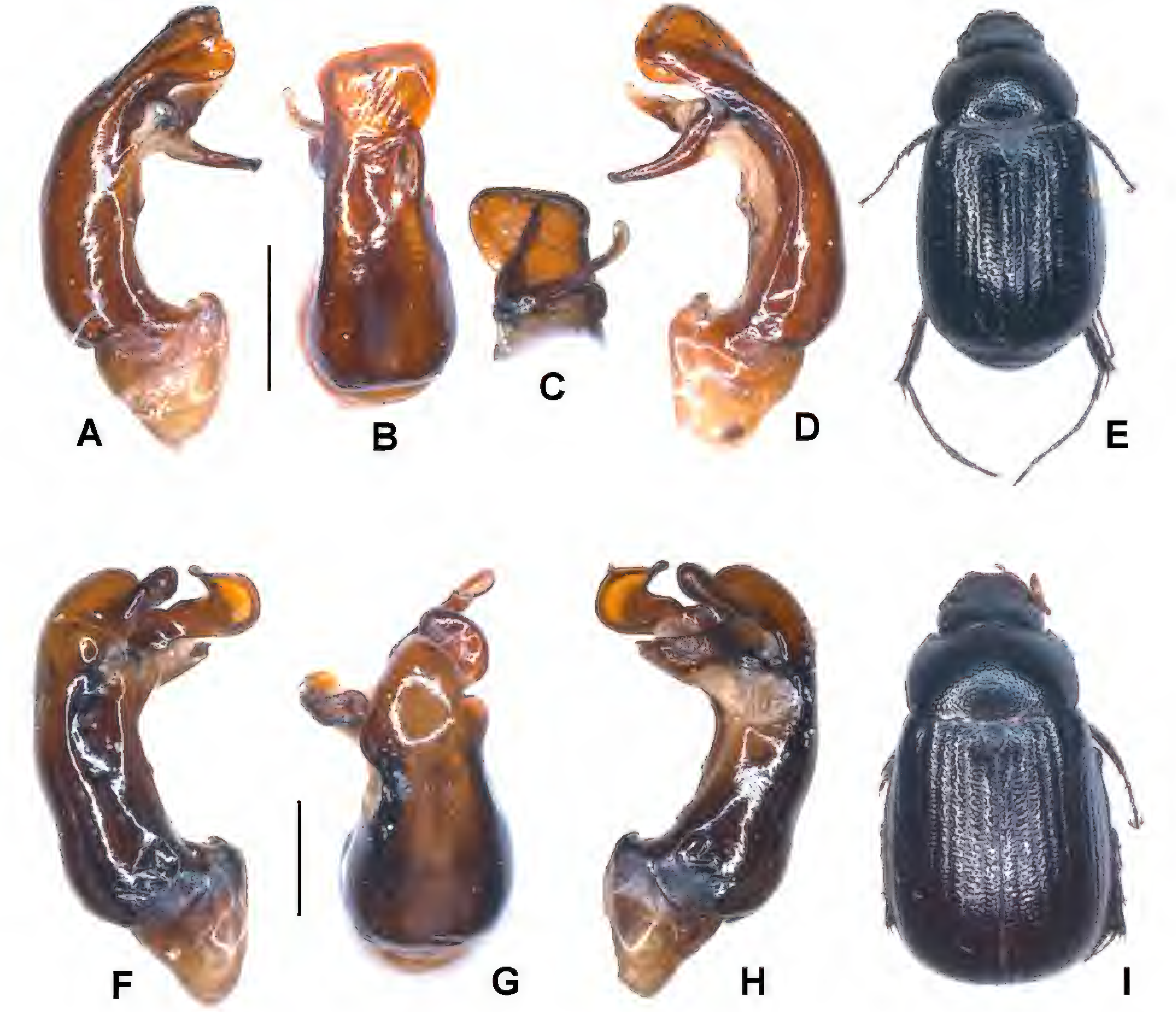

Fig 1. A–E. *Archeohomaloplia xiajuan* sp. nov. (holotype). **F–I**. *Archeohomaloplia volkovitchi* sp. nov., holotype. **A, F**. Aedeagus, left side lateral view. **D, H**. Aedeagus, right side lateral view. **B, G**. Aedeagus, dorsal view. **C**. Parameres, ventral view. **E, I**. Habitus (not to scale). Scale: 0.5 mm.

Archeohomaloplia volkovitchi sp. nov.

urn:lsid:zoobank.org:act:09195EA9-D30C-455C-8A60-68CB0E656644
Fig. 1

Type material examined. Holotype: ♂ "Yunnan 70km NNW Xiajuan 24.V.2002 Volkovitch/ Asia Sericini sp 1159" (ZIN). Paratypes: 1 ♂, 1 ♀ "Yunnan 70km NNW Xiajuan 20.V.2002 Volkovitch" (ZIN, ZFMK).

Description. Length: 5.9 mm, length of elytra: 4.0 mm, width: 3.1 mm. Body oblong, black, antenna black, dorsal surface shiny, with a few sparse short setae on elytra, otherwise glabrous.

Labroclypeus trapezoidal, widest at base and strongly convergent apically, lateral margins convex; anterior angles almost blunt, weakly rounded; lateral border and ocular canthus producing a blunt angle; margins moderately reflexed, anterior margin moderately emarginate medially; surface medially convex and moderately shiny, finely and densely punctate, distance between punctures less than their diameter, with a few robust punctures behind anterior margin bearing each a long, erect seta; frontoclypeal suture weakly incised and moderately curved; smooth area in front of eye approximately 1.3 × as wide as long; ocular canthus short and wide, subtriangular, rounded at apex, finely and densely punctate, without terminal seta. Frons shiny, with fine, dense punctures; with a single seta at the end of frontoclypeal suture beside eyes. Eyes small, ratio of diameter/interocular width: 0.51. Antenna brown, with ten antennomeres; club yellow, with three antennomeres, little longer than remaining antennomeres combined. Mentum weakly elevated and flattened anteriorly.

Pronotum moderately wide, widest at middle, lateral margins strongly curved and slightly convergent basally, but stronger convergent anteriorly; anterior angles strongly produced and sharp, posterior angles strongly rounded and almost obsolete; anterior margin convexly produced medially, with a broad marginal line; lateral basal margin with marginal line, otherwise without margin; surface with dense and fine punctures, glabrous and only with minute setae in punctures; anterior and lateral borders densely setose; hypomeron simple, not carinate at base and consequently not ventrally produced. Scutellum triangular and shiny, slightly longer than wide, with fine and dense punctures, with minute setae in punctures.

Elytra oblong, widest in apical third, striae weakly impressed, finely and densely punctate, intervals weakly convex, with fine, moderately dense punctures often concentrated along the striae, odd intervals with single, fine, short, yellow setae; interior apical angle of elytra with a short seta; epipleural edge fine ending at the strongly curved external apical angle of elytra, epipleura densely setose; apical border of elytra with a narrow membraneous rim of short microtrichomes.

Ventral surface shiny, with fine and moderately dense punctures, finely densely setose; metacoxa glabrous with a few fine, long, adjacent setae laterally only; abdominal sternites micro-reticulate, with an indistinct, transverse row of coarse punctures bearing a moderately long seta between fine, dense punctation, a few fine punctures bear a short seta; penultimate sternite apically with a smooth, sclerotized border which is one fifth as long as the sternite, last sternite medially 0.75 × as long as penultimate one. Mesosternum between mesocoxae as wide as mesofemur, with fine, long setae. Ratio of length of metepisternum/metacoxa: 1/1.44. Pygidium moderately evenly convex, finely and sparsely punctate, without smooth midline; surface shiny, only at apex with short setae.

Legs slender and moderately long; femora shiny, with two longitudinal rows of setae, coarsely but sparsely punctate; metafemur sharply carinate anteriorly and without a submarginal serrate line, posterior margin weakly convex and with a few short setae basally, its ventral part only weakly widened in apical half and not serrate, dorsal posterior margin not serrate, with dense, long setae. Metatibia slender and moderately long, evenly widened towards apex, ratio width/length: 1/3.2; dorsal margin sharply carinate, with two groups of spines, basal group at first quarter, apical group at two thirds of metatibial length, basally with a few single, fine setae; external face longitudinally convex, with coarse and dense punctures laterally, glabrous; ventral margin with a sharp, finely serrate margin, with four robust setae; internal face laterally with a few punctures bearing each a fine seta; apex interiorly deeply excavate at middle and not truncate near tarsal articulation. Meso- and metatarsomeres dorsally glabrous and finely densely punctate, ventrally with sparse, short setae; metatarsomeres ventrally with a finely serrate ridge, beside it with a robust longitudinal carina; metatarsomere 1 as long as following tarsomere and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate, protarsal claws symmetric.

Aedeagus: Fig. 1F–H. Habitus: 1I.

Diagnosis. *Archeohomaloplia volkovitchi* sp. nov. differs from all other *Archeohomaloplia* species by the complexly shaped dorsal apophysis of the phallobase which is bent several times around its axis.

Etymology. The species is named in honor of its collector V. Volkovitch (noun genitive case singular).

Variation. Length: 5.9–6.1 mm, length of elytra: 4.0–4.4 mm, width: 3.1–3.3 mm. Female: Antennal club distinctly shorter than the remaining antennomeres combined, eyes little smaller than in male: ratio of diameter/interocular width: 0.42; pygidium almost flat, impunctate in apical half, with a fine microstructure.

Archeohomaloplia frolovi Ahrens, 2011

Additional material examined. 2 ♂♂ “Dol. r. Tunk-go-ho 22-VII-93 Potanin/ Paratypus Arch. medvedevi Nikolajev 1982” (ZIN).

Updated key to the species of *Archeohomaloplia* (♂♂)

1 Hypomeron not carinate. Metatarsomere 1 shorter than the following tarsomere. Elytra and legs black 2
1’ Hypomeron finely carinate. Metatarsomere 1 longer than the following tarsomere. Elytra dark brown, legs brownish 14
2 Disc of pronotum with numerous long, erect setae 3
2’ Disc of pronotum without long setae. 7
3 Setae on pronotum and elytra long, twice as long as ocular diameter .... ***A. frolovi*** Ahrens, 2011
3’ Setae on pronotum and elytra moderately long, as long as ocular diameter 4
4 Dorsal apophysis of aedeagus narrow 5
4’ Dorsal apophysis of aedeagus wide and truncate at apex .... ***A. xiajuan*** sp. nov.
5 Dorsal apophysis of aedeagus moderately long and straight (dorsal view). Setae on elytra shorter than intervals wide. Posterior angles of pronotum blunt. 6
5’ Dorsal apophysis of aedeagus strongly bent backwards at middle forming a sharp hook. Setae on elytra almost as long as intervals wide. Posterior angles of pronotum obsolete .... ***A. hebashana*** Ahrens, 2011

6 Right paramere strongly bent twice, behind basal third and shortly before apex .... ***A. yunnana*** (Miyake & Yamaya, 2001)
6’ Right paramere strongly bent once only, behind basal third .... ***A. ganhaiziensis*** Ahrens, 2011
7 Basal marginal line almost complete medially 8
7’ Basal marginal line widely interrupted medially... 12
8 Sides of clypeus strongly convex, basally slightly convergent, showing a distinct angle with the ocular canthus. Body size larger than 7 mm. Aedeagus with large lateral apophysis .... ***A. abbreviata*** (Fairmaire, 1897)
8’ Clypeus widest at base, angle between sides of clypeus and ocular canthus blunt and indistinct. Body size smaller than 6 mm 9
9 Tegument of pronotum smooth and very shiny. ... 10
9’ Tegument of pronotum micro-reticulate (80x) and slightly dull .... ***A. kalabi*** Ahrens, 2011
10 Dorsal apophysis of phallobase short, much shorter than the apex of phallobase wide .... ***A. nikolajevi*** Ahrens, 2011
10’ Dorsal apophysis of phallobase long, almost as wide as the apex of phallobase 11
11 Posterior angles of pronotum and anterior angles of labroclypeus blunt ..... ***A. medvedevi*** Nikolajev, 1982
11’ Posterior angles of pronotum obsolete. Anterior angles of labroclypeus convex .... ***A. yaregongensis*** Ahrens, 2011
12 Setae on elytra distinctly shorter than elytral intervals wide. Dorsal apophysis of phallobase wide at base 13
12’ Setae on elytra as long as elytral intervals wide. Dorsal apophysis of phallobase all over narrow and tube-shaped .... ***A. safraneki*** Ahrens, 2011
13 Dorsal apophysis of phallobase simple, not reflexed around its axis, sharply narrowed and pointed at apex. Right paramere divided in a dorsal and ventral lobe .... ***A. mingi*** Ahrens, 2011
13’ Dorsal apophysis of phallobase reflexed around its axis, not sharply narrowed and pointed at apex. Right paramere simple, not divided in a dorsal and ventral lobe .... ***A. volkovitchi*** sp. nov.
14 Antennal club slightly reflexed, almost twice as long as the remaining antennomeres combined. Tibiae and tarsi yellowish brown .... ***A. taunggyiensis*** Ahrens, 2011
14’ Antennal club straight, almost 1.5 × as long as the remaining antennomeres combined. Tibiae and tarsi brown .... ***A. acuta*** Ahrens, 2011

DISCUSSION

The two newly discovered species raise the species count of known *Archeohomaloplia* taxa to 15. In the only so far existing comprehensive molecular phylogeny (Eberle et al. 2017), which also includes *Archeohomaloplia*, the genus resulted to be an ancestral lineage of a major clade of lineages composed mainly of species from the Indomalayan archipelago (e.g., including *Trioserica* Moser, 1922, *Neoserica* Brenske, 1894 sensu lato, *Tetraserica* Ahrens 2004, and *Microserica* Brenske, 1894). Most other species of the Asian mainland are part of a second clade, which is sister to the first one. Some lineages of this clade also colonized Africa and Northern America. All this makes the genus *Archeohomaloplia* particularly interesting from biogeographical point of view, especially also its relics-like occurrence in Yunnan and northern Indochina.

While the number of species of the genus *Archeohomaloplia* slightly increased with this contribution, this, however, changes very little in the asymmetric relation of species number compared to its sister clade in this first mentioned clade. Here, *Archeohomaloplia* is contrasted by several hundreds of species. The current study may contribute only little to resolve the questions about the causalities of these patterns of asymmetric diversity; however, small-scale biogeographical problems have been addressed only to a very limited extent (Liu et al. 2015b), mainly based on phylogenies with morphological characters (Ahrens 2006a, c, 2007c, 2009) which might be strongly under the impact of homoplasy of many morphological features. Given that existing molecular phylogenies are in large based on mitochondrial DNA, it appears premature to drive at this stage any conclusions, since many nodes of the phylogeny by Eberle et al. (2017) are yet poorly supported or even unresolved. Also, better sampling within the genus for molecular data would be desirable to test properly the monophyly of *Archeohomaloplia* – all tasks for future phylogenetic analyses of the group and the tribe.

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Scientific note

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Rediscovery of *Hyles svetlana* Shovkoon, 2010 (Lepidoptera: Sphingidae) from Kyzyl-Kum desert, Uzbekistan

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Abstract. Thirty-six years after the last published record of *Hyles svetlana* in Uzbekistan, we found the species at multiple locations in the Kyzl-Kum desert in 2022. Furthermore, we discovered larvae feeding on *Eremurus anisopterus* pointing to a possible oligophagous nature of *H. svetlana*, as described in early days, when it was still considered a desert population of *H. centralasiae*. We found phenotypes in both larva and imago of *H. svetlana* which appeared to be more similar to *Hyles euphorbiae*, giving rise to more questions regarding the relationships within the genus *Hyles* and the genetic identity of *H. svetlana*.

Keywords. *Hyles*, *Hyles svetlana*, Sphingid, Central Asia, Uzbekistan, Lepidoptera.

The distribution of *Hyles svetlana* Shovkoon, 2010 is understudied in Uzbekistan, since only a few collection sites have been published. The original description of this taxon was only in 2010 by Shovkoon. The populations were considered *Hyles centralasiae* (Staudinger, 1887) before the observations of significant differences in life-history traits (flight time, food plant and larval development) and phenotypic differences in the larvae compared to *H. centralasiae* were reported (Shovkoon 2010). A phylogenetic analysis of neutral mitochondrial markers confirmed a specimen of the type series and additional individuals from the type location in Kazakhstan (Aqtobe region) as part of the *H. siehei* clade (Hundsdoerfer et al. 2009), which is why the taxon was first described as a subspecies of *H. siehei*. These specimens formed a monophyletic clade only together with other specimens of *H. siehei* and those from the more southerly Plateau Ustyurt (also in Kazakhstan, 43°44'53.2" N, 53°38'13.5" E).

Nevertheless, de Freina & Geck (2014) raised the taxon to full species status. Thus it is currently referred to as *H. svetlana*, despite the lack of monophyletic clade formation based on mitochondrial DNA sequences (Hundsdoerfer et al. 2009). De Freina & Geck (2014) characterised the species as inhabiting semiarid to semihumid steppe and desert areas in a distribution range east of the Caspian Sea. The core area is the Shagyrai Plateau in the Kazakh Aqtobe region, the regions Qyzlorda, Mangistau, the Donyztau Plateau, and the Bolsheye Barsuki Sands, the Ustyurt Plateau in the border region between Southern Kazakhstan, Western Uzbekistan and Northwestern Turkmenistan. Furthermore, the eastern distribution area of *H. svetlana* was extended by R. Yakovlev (2017) to the Mongolian Bajtag-Bogd-Uul mountains (Fig. 1).

The last described finding of *H. svetlana* in Uzbekistan was by Falkovich in 1986 in the Kyzyl-Kum desert, reported as *H. centralasiae*. Before that, it was only found once in Uzbekistan in 1974, likewise in the Kyzyl-Kum desert.

We made two field trips in 2021 and 2022. In 2021 we arrived in the Kyzyl-Kum desert on the 11th of June, where no specimens could be observed. Contrary to the description of flowering time given in the original description of *H. svetlana*, the foodplant *Eremurus inderiensis* (Steven, 1832) was already desiccated when we arrived at sites where it was expected. The precocious development of the foodplant was likely due to the earlier spring leaf emergence (i.e., earlier spring greening) caused by the ongoing Anthropocene climate change (Barichivich et al.

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Table 1. Overview of *Hyles svetlana* specimens found between 1–8 May 2022 in the Kyzyl-Kum desert.

date	place	adult	larva	foodplant
02.05.2022	Kyzylkum desert	–	23	*Eremerus inderensis*
02.05.2022	Kyzylkum desert	–	18	*Eremerus inderensis*
02.05.2022	Kyzylkum desert	1	23	*Eremerus inderensis*
03.05.2022	Shor Kul	5	–	–
08.05.2022	Kyzylkum desert	–	10	*Eremerus inderensis*
08.05.2022	Kyzylkum desert	–	5	*Eremerus anisopterus*
08.05.2022	Kyzylkum desert	–	5	*Eremerus inderensis*
08.05.2022	Kyzylkum desert	–	34	*Eremerus inderensis*
08.05.2022	Kyzylkum desert	–	7	*Eremerus inderensis*
08.05.2022	Kyzylkum desert	–	6	*Eremerus inderensis*
08.05.2022	Kyzylkum desert	–	1	*Eremerus inderensis*

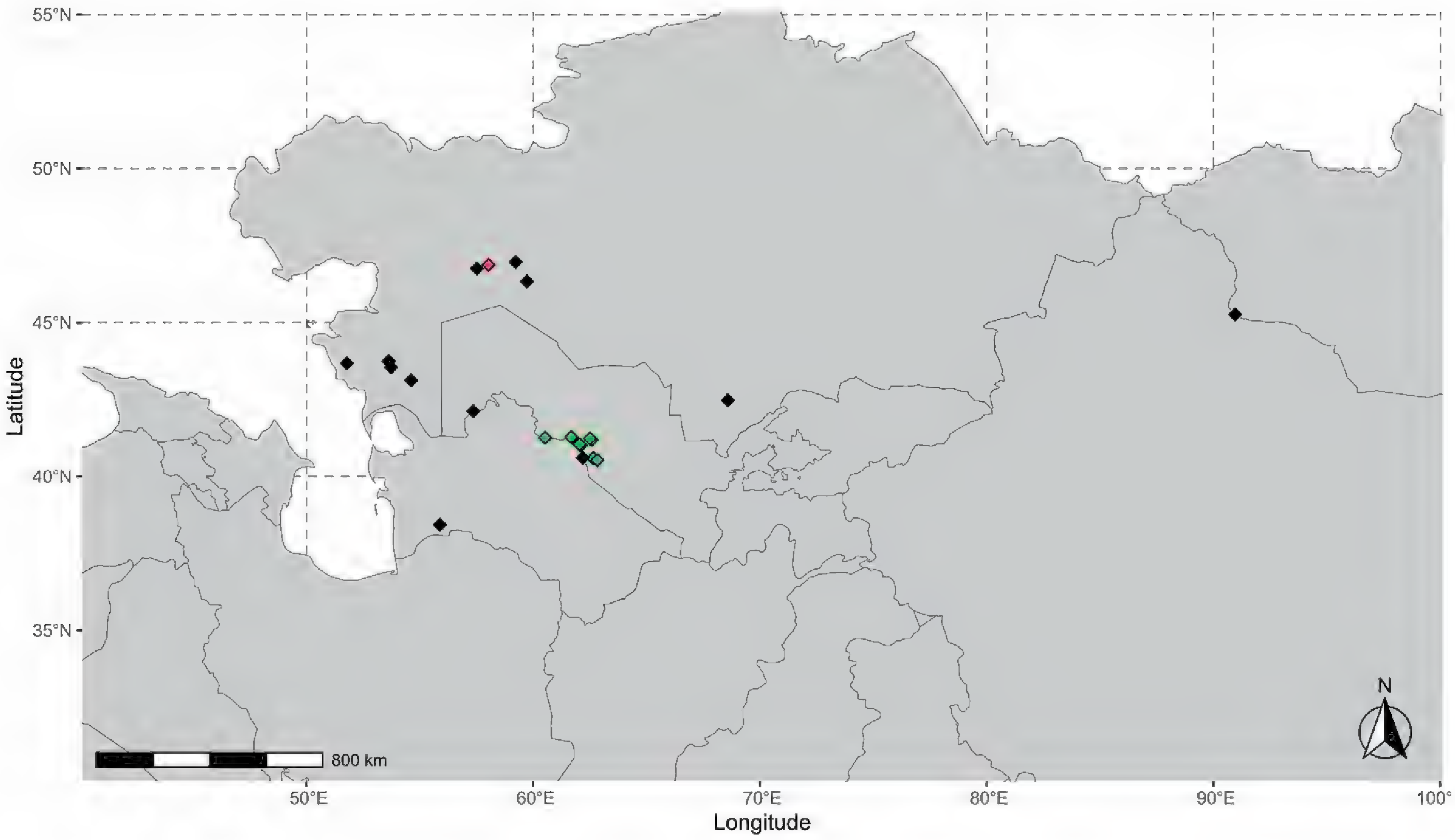

Fig. 1. Map of the localities in Central Asia where *Hyyles svetlana* was observed. The dots in green are the locations where we found *H. svetlana*. Black are localities which other authors described (Yakovlev et al. 2017, de Freina & Geck 2014). The locality in red is the type locality in western Kazakhstan (Shagyray Plateau, Aktobe region).

2013; Piao et al. 2015; Liu et al. 2016). However, we found typical larval excretions and feeding marks on the plants, so we came back earlier the subsequent year.

In 2022, we found 138 specimens of *H. svetlana* over eight days (1–8 May 2022), of which 132 individuals were larvae, and six individuals were imagos (Table 1).

They were either collected with the flower spike of the foodplant to enable further larval development or preserved in ethanol for further research. The imagos were collected using a mercury-vapour lamp and white linen placed beneath the light. Although extensive search in the Karakalpakistan region was done, we found *H. svetlana* only at the sites marked in Fig. 1. The material collected is deposited in the Senckenberg Natural History Collections in Dresden, Germany, and the Zoological Institute, Academy of Science Uzbekistan in Tashkent, Uzbekistan.

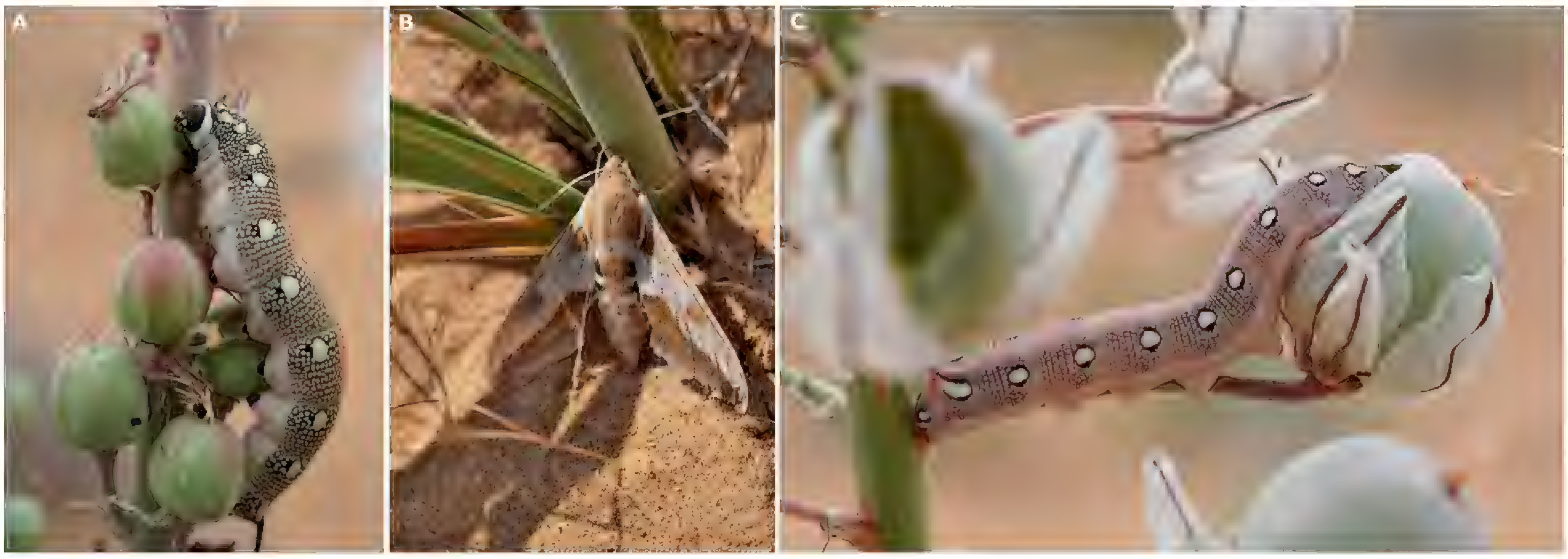

Fig. 2. Common phenotype of *Hyles svetlana*. **A**. Larva. **B**. Imago. **C**. Larva feeding on *Eremurus anisopterus*.

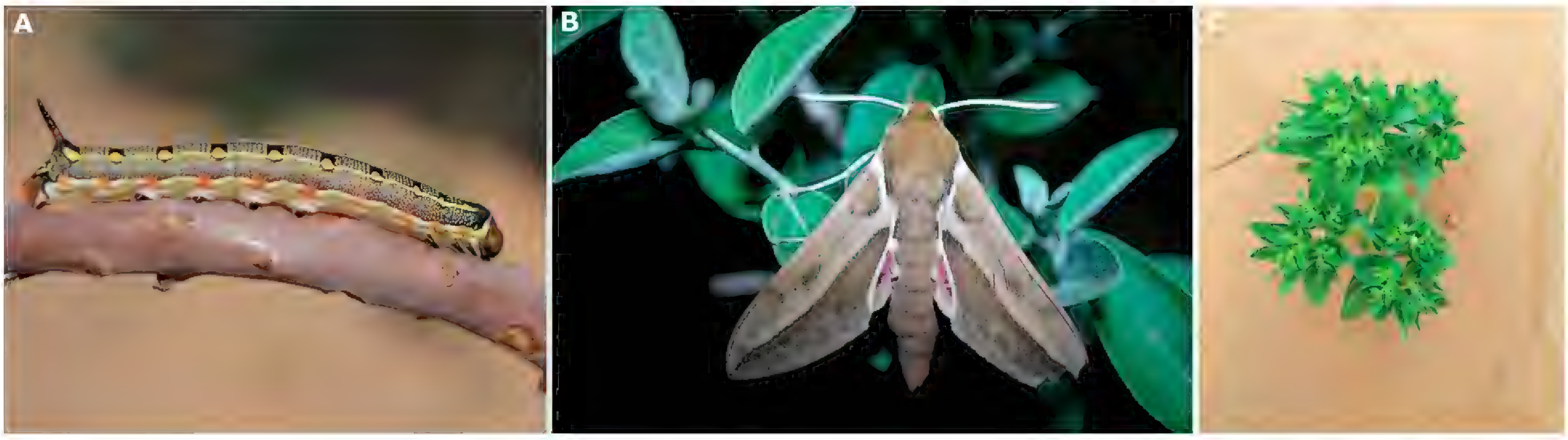

Fig. 3. Rare phenotypes of *Hyles svetlana*. **A**. Larva. **B**. Imago resembling *H. euphorbiae*. **C**. Plant of the genus *Euphorbia* found close to caterpillar localities in the Kyzyl-Kum desert.

When we arrived, the food plant already showed completely developed seed capsules, contrary to the expected flower spikes, indicating an earlier flowering period in 2022. We found all developmental stages of *H. svetlana,* from eggs laid directly on the fruit capsules, over different larval stages to imagos, coming to light during the night (except for pupae, Fig. 2 A–B). All specimens were collected from or close to *Eremurus inderiensis* and *Eremurus anisopterus* (Karelin & Kirilov, 1842). We observed *H. svetlana* larvae feeding on *Eremurus anisopterus* (Fig. 2C). Until now, *H. svetlana* was described as monophagous for *E. inderiensis* by the original subspecies description. In contrast, our observation points to a possible oligophagous nature of *H. svetlana* on different species of *Eremurus*, as described in Shchetkin (1952, 1975) when *H. svetlana* was still considered a desert population of *H. centralasiae*. Additionally, the *H. svetlana* larvae were indifferent to food sources (fruit capsules compared to flowers), while those of *H. centralasiae* were reluctant to feed on fruit capsules in 2021 (pers. obs.).

At the collection sites, we found all developmental stages of larvae, of which some differed from the phenotype described by Shovkoon (2010) and Shchetkin (1952, 1960, 1975). Besides the light-rosé coloured phenotype (Fig. 2A), we found a variation that appeared to be a mixture of the typical light-rosé coloured phenotype of *H. svetlana* and the green-coloured *Hyles euphorbiae* (Linnaeus, 1758) (Fig. 3A). The finding of this phenotype gives room for speculations about possible hybridisation events and their regularity. Even more so, as we found plants of the genus *Euphorbia* (Fig. 3C) and uncommonly marked imagos (possibly either *H. svetlana* or *H. euphorbiae*) close to the collection sites (Fig. 3B). This unexpected finding opens more questions regarding the genus *Hyles*. Further research on the genetic identity of *H. svetlana* is needed.

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Research article

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New records of Japanese robber flies (Diptera: Asilidae) deposited at the ZFMK collections

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Abstract. Robber flies are a species-rich family of insects and, therefore, pose a challenge for biodiversity research. Museum collections can help to shed light on diversity patterns and to tackle ecological questions. However, in order to be used by the scientific community, collections need to be visible and accessible. Here we present the previously unidentified Asilidae specimens collected in Japan held in the collections of the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. Our material was collected by Bradley Sinclair during the 1990ies using a hand net and by Alexander Blanke between 2014 and 2016 using Malaise traps. We identified 334 individuals belonging to 20 named species and one unnamed taxon. Altogether, these holdings represent 19.4% of the known Japanese asilid fauna. Malaise traps used by Blanke were placed at the Sugadaira Research Station of the University of Tsukuba, Ueda, Nagano, and they sampled 16 species (15.4% of the Japanese fauna). The collection of Sinclair stems mainly from Kyushu Island. *Stichopogon gracilifemur* Nagatomi, 1983 is recorded for the first time from the island of Kyushu. All recorded species are featured with high-quality color images and information on synonymy, types, literature and distribution is also provided.

Key words. Assassin flies, Japan, Kyushu, Sugadaira Research Station, malaise trap, ZFMK Collections.

INTRODUCTION

Commonly known as robber flies or assassin flies, the Asilidae (Insecta: Diptera: Brachycera) form one of the largest families of Diptera, with more than 7,500 described species worldwide (Dikow 2020). Within the suborder Brachycera, they belong to the infraorder Muscomorpha and the superfamily Asiloidea, in which they are most closely related to Mydidae, Apioceridae and Therevidae (Dikow 2009). Because of their comparably large size and their conspicuous behavior as sit-and-wait predators, robber flies have caught the interest of many dipterists and naturalists. Asilids inhabit every continent except Antarctica and occupy diverse habitats (Hull 1962). Although they are most diverse in hot and dry environments with sandy soils, they can be found from tropical lowland forests up to alpine regions at 4,500m altitude (Hull 1962).

All robber fly larvae and adults are predatory on arthropods. Adults usually catch the prey in flight, except members of Leptogastrinae, who actively search and catch also substrate bound prey (Wolff et al. 2018). Because of their predatory behavior, a few authors have analyzed the potential ecosystem services provided by robber flies and hereby mainly focused on their ability to feed on arthropods harmful to forestry (Kinoshita 1940; Wichmann 1956). Wei et al. (1995) found significant effects of larvae of *Promachus yesonicus* Bigot, 1887 on wheat-feeding scarabaeid beetles. Furthermore, robber flies are interwoven into complex food webs and may help to stabilize them and they can serve as indicator species for different habitat qualities (Wolff et al. 2018).

In the present study we identified the Asilidae specimens from Japan present in the collections of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn (Germany). Japan is formed by over 6,800 large to very small islands and extends in a 3,800 km long arch from the Sea of Okhotsk in the north to the East China Sea in the south (Embassy of Japan 2020). Therefore, it contains a wide variety of climates and a habitat diversity that is even enlarged by the strong altitudinal differences between the coastline and the mountainous regions. Our samples only cover a small part of the geographical range and are mainly taken from or nearby woodlands, which cover approximately 73% of the country (Embassy of Japan 2020). For Japan, Utsuki (2014) lists 104 species of robber flies, which are classified in 41 genera from 13 subfamilies.

The present study aims to increase the visibility of the Asilidae collection at the ZFMK and help towards a bet-

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ter understanding of the Japanese robber fly fauna. We provide high-quality images for at least one sex of every studied species to facilitate the identification of the taxa in future studies.

MATERIAL AND METHODS

Material

The material was collected in the last 30 years by Alexander Blanke and Bradley Sinclair. We examined all previously unidentified Japanese asilid specimens deposited in the ZFMK collections. A total of 334 specimens were examined. Out of these, 314 were collected by Alexander Blanke from 2014 to 2015, using Malaise traps. Trapping took place from 21 Jul. 2014 to 2 Sep. 2014, from 19 Apr. 2015 to 7 Jun. 2015, and from 26 Apr. 2016 to 3 May 2016. The traps were set at two locations in the property of the Sugadaira Research Station of the University of Tsukuba (Ueda, Nagano Prefecture) (see Table 1). The first site (B1) is located on a six-hectare semi-natural grassland with an Andosol soil that is managed by the research station by harvesting the grass once a year in autumn (SMRC 2020). The second site (B2) at the Sugadaira Research Station is located ca. 200 m from the first site in an approximately 50 years old succession forest that is dominated by red pine, *Pinus densiflora* Siebold & Zucc. and covers an area of 8.5 hectares (SMRC 2020). The Malaise traps operated with 96% ethanol. Collected specimens were preserved in 96% ethanol and subsequently dried with a critical point drier in order to be mounted on a pin.

The other 20 studied specimens were collected by Bradley Sinclair in the years 1997 and 1999. All but one stem from Kyushu Island, either from Fukuoka Prefecture or Kumamoto Prefecture (see Table 1). One specimen was collected on Okinawa. According to Sinclair, all specimens were collected with a sweep net at a stream or the nearby vegetation when he was collecting aquatic Empididae. Most of them were collected in forested areas. For a list of all locations see Table 1.

Terminology and literature

Terminology follows Cumming & Wood (2017) and the systematic classification of Asilidae follows Dikow (2009). Faunistic information is mainly taken from Utsuki (2014). Sampling localities are listed in Table 1. The literature used for species identification is listed under the respective species (see Results). Synonymy information and information on the type locality are mostly taken from Lehr (1988). Information on collections holding types were kindly provided by Fritz Geller-Grimm (unpublished, abbreviated as GG) or taken from Evenhuis & Pape (2020) (*Sytema Dipterorum* database at http://diptera.org/, abbreviated as SD).

Institutional abbreviations

BMNH =	The Natural History Museum, London, UK
EIHU =	Hokkaido University, Sapporo, Japan

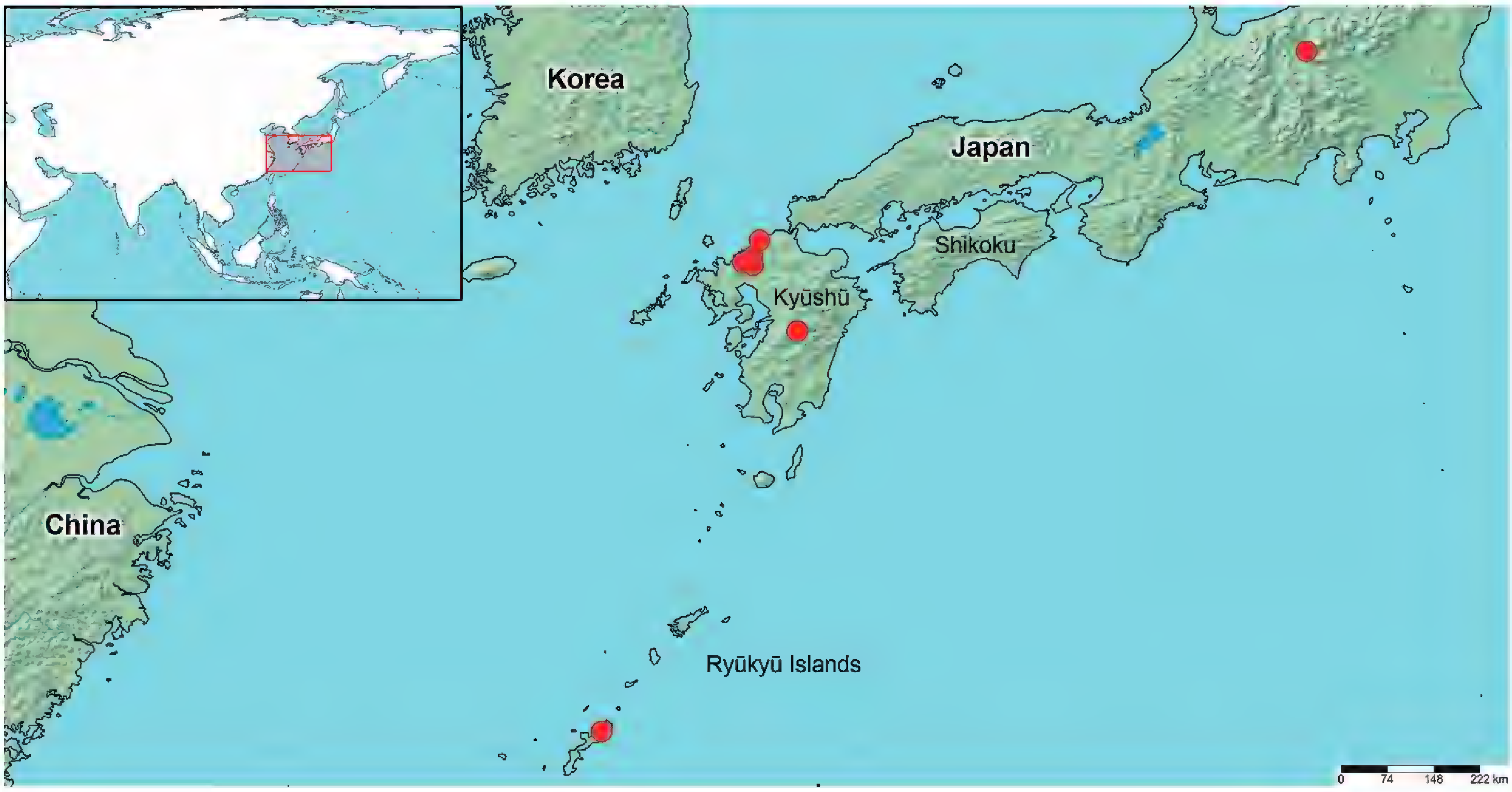

Fig. 1. Distribution map of the sampling localities in Japan.

Table 1. List of sampling localities In Japan by Sinclair and Blanke (see Fig. 1).

Area/State	City	Locality	Lat	Long	Ecology	Altitude	Collector
Nagano Prefecture	Ueda	Sugadaira Kogen, near SMRC	36,52389	138,34944	Grassland (B1)	1330 m	Blanke A.
Nagano Prefecture	Ueda	Sugadaira Kogen, near SMRC	36,52167	138,35083	Forest (B2)	1335 m	Blanke A.
Fukuoka Prefecture	Fukuoka	Chayama	33,56138	130,36638			Sinclair B.J.
Fukuoka Prefecture		Mount Sefuri			Beech	1000 m	Sinclair B.J.
Fukuoka Prefecture	Fukuoka	Nogochi			Forest	260 m	Sinclair B.J.
Kumamoto Prefecture		Itsuki-mura					Sinclair B.J.
Kumamoto Prefecture		Mt Raizan, Maebaru-shi				500-600 m	Sinclair B.J.
Kumamoto Prefecture		Izumi-mura, Siibagoe			Hardwood forest	1250 m	Sinclair B.J.
Kumamoto Prefecture		Shiiba-goe			Hardwood forest	1250 m	Sinclair B.J.
Okinawa		Hiji Falls			Hardwood forest		Sinclair B.J.

EUMJ = Laboratory of Environmental Entomology, Faculty of Agriculture, Ehime University, Matsuyama, Japan
PAN = Polish Academy of Science, Museum of the Institute of Zoology, Wilcza 64, Warsaw 00-679, Poland
TMUZ = Department of Biological Sciences, Tokyo Metropolitan University, Tokyo, Japan
USNM = National Museum of Natural History, Washington D.C., USA
ZMUC = Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark
ZSMC = Zoologische Staatssammlung München, Munich, Germany

Technical equipment

Specimens were examined using a Nikon SMZ1500 stereo microscope. For photography we used a Canon EOS 7D® mounted on a P-51 Cam-Lift (Dun Inc., VA, USA), supported by Adobe Lightroom® ver. 5.6. Serial photographs were stacked using Zerene Stacker® ver. 1.04 software (Richland, WA, USA). Maps were created with Simple-Mappr (Shorthouse 2010).

RESULTS

We studied a total of 334 specimens, belonging to 20 species and one unnamed taxon (see Appendix I). They represent 15 genera from eight subfamilies. The Malaise traps at Sugadaira-Kogen yielded 314 robber fly specimens belonging to 16 species. No robber fly was collected in 2016. The remaining 20 specimens of seven species were collected by Sinclair. Detailed information and unique identifiers are provided for each specimen in the Appendix 1. Under each species, we mention the locality, the date and the number of studied specimens between brackets (see New records).

The three species with the largest number of individuals were *Molobratia sapporensis* (Matsumura, 1916) (110), *Neoitamus angusticornis* (Loew, 1858) (68) and *Eutolmus koreanus* Hradský & Hüttinger, 1985 (25). All of these were collected in the Malaise traps at the Sugadaira Research Station, with the exception of four specimens of *Neoitamus angusticornis* that were collected by Bradley Sinclair. 103 specimens from 13 species were sampled in the forest site and 210 specimens of 13 species came from the grassland site. *Cyrtopogon pictipennis* Coquillett, 1898, *Trichomachimus scutellaris* (Coquillett, 1898) and *Neoitamus ishiharai* Tagawa, 1981 were sampled exclusively from the forest site, while *Choerades* sp., *Philonicus nagatomii* Utsuki, 2008 and *Promachus yesonicus* Bigot, 1887 were sampled only in the grassland site.

All studied records (Fig. 1) lay inside the previously known distribution ranges of the taxa, except the record of *Stichopogon gracilifemur* Nagatomi, 1983 from Itsuki-mura, which is a new distribution record for Kyushu.

A list of our records follows organized by alphabetical order of the subfamilies and genera. Ambiguous identi-

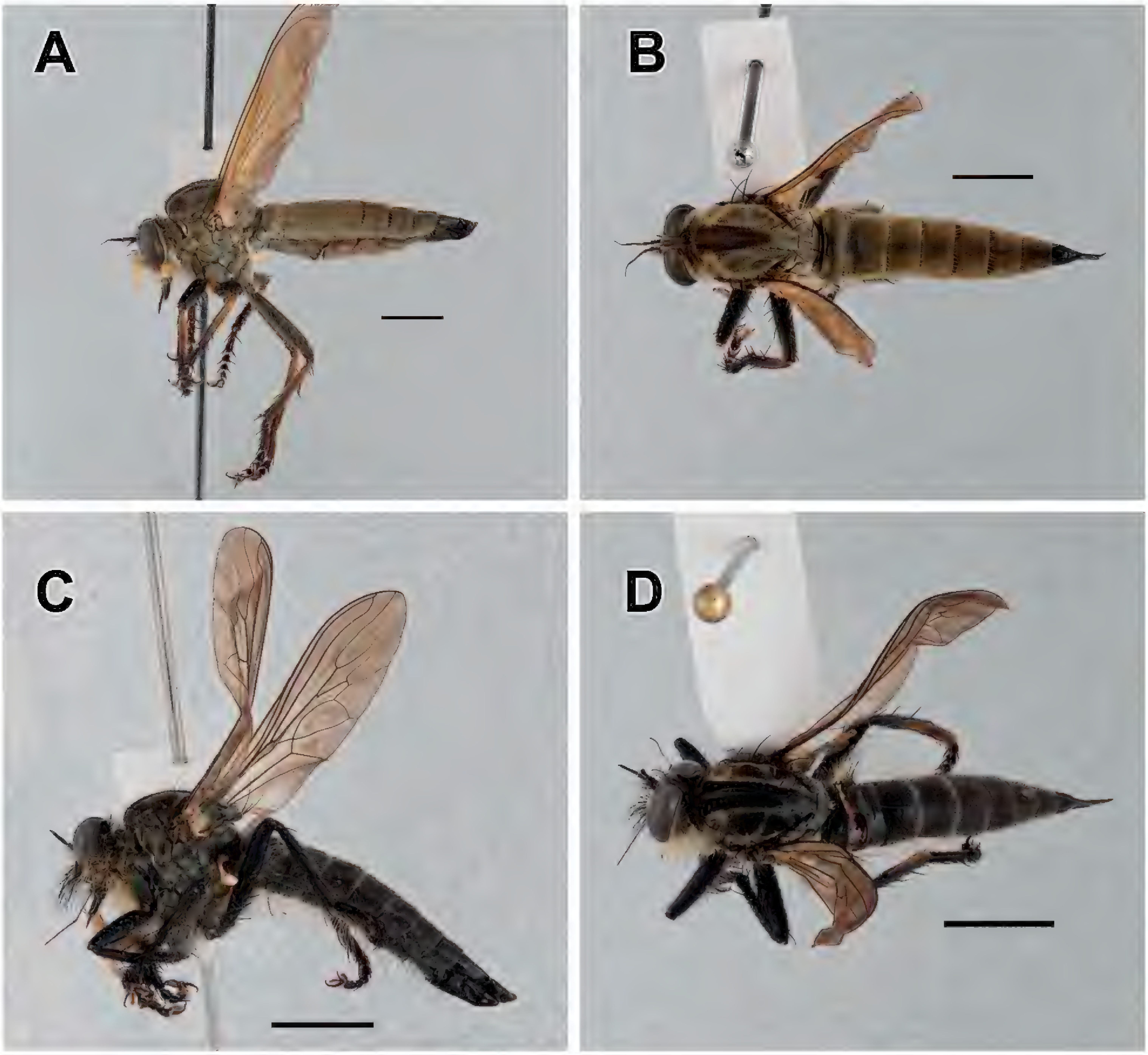

Fig. 2. A–B. *Eutolmus brevistylus* (Coquillett, 1898), female habitus. **A.** Lateral view. **B**. Dorsal view. **C–D**. *Eutolmus koreanus* Hradský & Hüttinger, 1985, female habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

fications and observations are discussed under each species (see Remarks) if necessary.

Asilinae

Eutolmus Loew, 1848
Eutolmus brevistylus (Coquillett, 1898)
Fig. 2A–B
Asilus brevistylus Coquillett, 1898. Proc. U.S. Natl. Mus. 21: 314 – Type locality: Japan – Type collection: USNM [SD].
Eutolmus ussuriensis Engel, 1928. Fliegen pal. Reg., 4 (2): 148 – Type-locality: "Kolowska am Ussuri" (Russia, Far East) – Type collection: unknown.

References for identification. Young (2006), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–05 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (3); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (10); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (7); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 2–11 Aug. 2014 (2).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu; Russian Far East; China; Korean Peninsula.

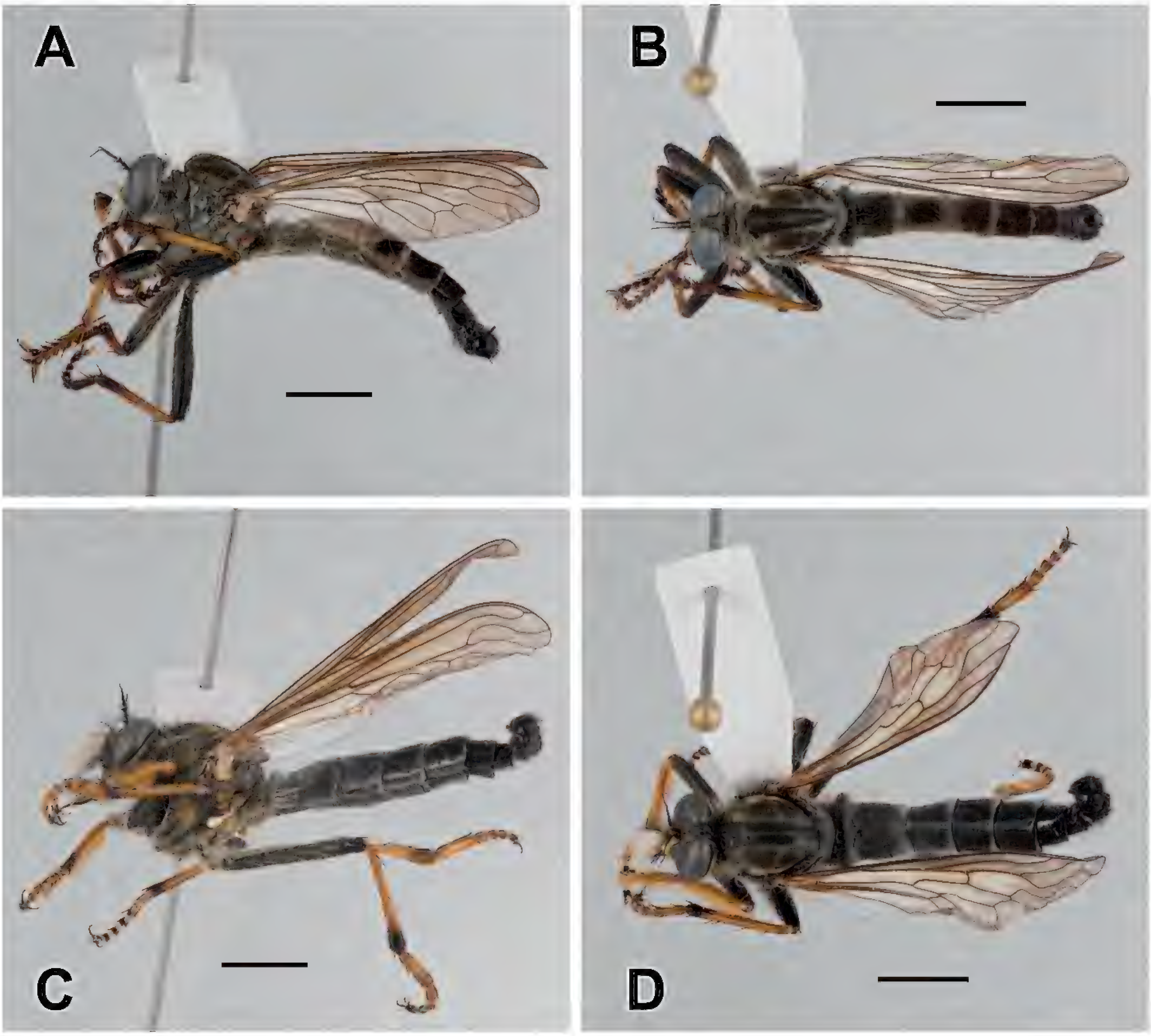

Fig. 3. A–B. *Neoitamus angusticornis* (Loew, 1858), male habitus. **A**. Lateral view. **B**. Dorsal view. **C–D**. *Neoitamus castaneipennis* Tagawa, 1981, male habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

Eutolmus koreanus Hradský & Hüttinger, 1985
Fig. 2C–D

Eutolmus koreanus Hradský & Huttinger, 1985. Entomofauna 6: 170 – Type locality: South Korea: Myohyang Mts. & Onpho an Chongjin – Type collection: PAN.

References for identification. Hradský & Hüttinger (1985), Young (2006), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 21–29 Jun. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (2); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (13); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–02 Aug. 2014 (4); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (3); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 2–11 Aug. 2014 (1).

Distribution. Japan: Honshu; Korean Peninsula.

Neoitamus Osten-Sacken, 1878

Neoitamus angusticornis (Loew, 1858)
Fig. 3A–B

Itamus angusticornis Loew, 1858. Wiener Entomol. Mon. 2: 106 – Type locality: "Japan" – Type collection: unknown.

References for identification. Ohishi & Tagawa (1997), Young (2006), Tagawa (2020).

New records. Fukuoka Pref., Fukuoka, Nogochi: 7 Jun. 1997 (1); Kumamoto Pref., Mt Raizan, Maebaru-shi: 14 Jun. 1997 (2); Nagano Pref., Ueda, Sugadaira

Research Station, grassland (B1): 21–29 Jun. 2014 (3); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 21–29 Jun. 2014 (3); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–05 Jul. 2014 (16); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (15); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (7); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (6); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (8); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 2–11 Aug. 2014 (6); Kumamoto Pref., Shiiba-goe: 24 Aug. 1997 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Shikoku, Kyushu; Russia: Sakhalin.

Neoitamus castaneipennis Tagawa, 1981
Figs 3C–D

Neoitamus castaneipennis Tagawa, 1981. Trans. Shikoku Entomol. Soc. 15: 195 – Type locality: Japan: Ehime Pref., Matsuyama, Komenono – Type collection: EUMJ.

References for identification. Ohishi & Tagawa (1997), Tagawa (1981), Young (2006), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 17–24 May 2015 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 24–31 May 2015 (7); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 21–29 Jun. 2014 (6); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 21–29 Jun. 2014 (2); Nagano Pref., Ueda, Suga-

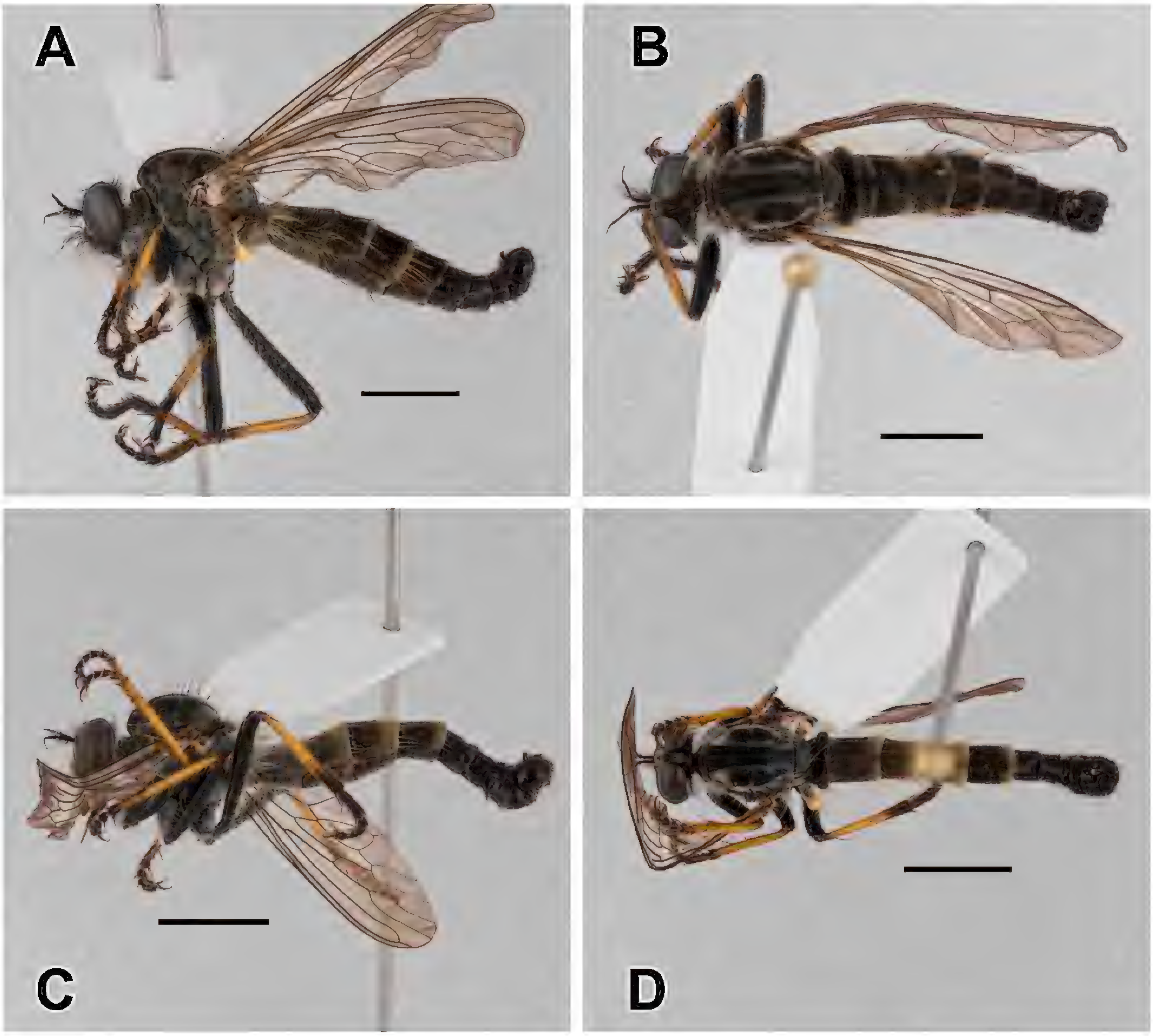

Fig. 4. A–B. *Neoitamus univittatus* (Loew, 1871), male habitus. **A**. Lateral view. **B**. Dorsal view. **C–D**. *Neoitamus ishiharai* Tagawa, 1981, male habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

daira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (4).

Distribution. Japan: Honshu, Shikoku.

Neoitamus univittatus (Loew, 1871)
Fig. 4A–B

Itamus univittatus Loew, 1871. Syst. Besch. 9 Theil, 2 Band: 183 – Type locality: Russia: Irkutsk – Type collection: unknown.

References for identification. Ohishi & Tagawa (1997), Young (2006), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 21–29 Jun. 2014 (7): Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (6).

Distribution. Japan: Honshu, Shikoku; Russia; Kazakhstan; Mongolia.

Neoitamus ishiharai Tagawa, 1981
Fig. 4C–D

Neoitamus ishiharai Tagawa, 1981. Trans. Shikoku Entomol. Soc. 15: 201 – Type locality: Japan: Tokushima Pref., Mt Tsurugi – Type collection: EUMJ.

References for identification. Ohishi & Tagawa (1997), Tagawa (1981), Young (2006), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (1).

Distribution. Japan: Honshu, Shikoku.

Philonicus Loew, 1849
Philonicus nagatomii Utsuki, 2008
Fig. 5A–B

Philonicus nagatomii Utsuki, 2008. Jpn. J. Syst. Ent.: 53 – Type locality: Japan: Honshu, Tochigi Pref., side of River Kinu-gawa, Ishii-machi, Utsunomiya-shi – Type collection: TMUZ.

References for identification. Young (2006), Utsuki (2008).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 11–23 Aug. 2014 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu.

Remarks. Utsuki (2008) described *P. nagatomii* as very similar to *Philonicus albiceps* (Meigen, 1820), except that it possesses a longer distiphallus. The distiphallus of our specimen matches the description of the one of *P. nagatomii*.

Promachus Loew, 1848
Promachus yesonicus Bigot, 1887
Fig. 6A–B

Promachus yesonicus Bigot, 1887. Bull. Soc. entomol. Fr. (6) 7: lxxix – Type locality: Japan: north of Yeso – Type collection: unknown.

Promachus jesonicus: Paramonov (1931): 228, misspelling.

References for identification. Paramonov (1931), Young & Hradský (2008).

New records. Fukuoka Pref., Fukuoka, Chayama: 20 Jun. 1999 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 2–11 Aug. 2014 (2); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 11–23 Aug. 2014 (4); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1):

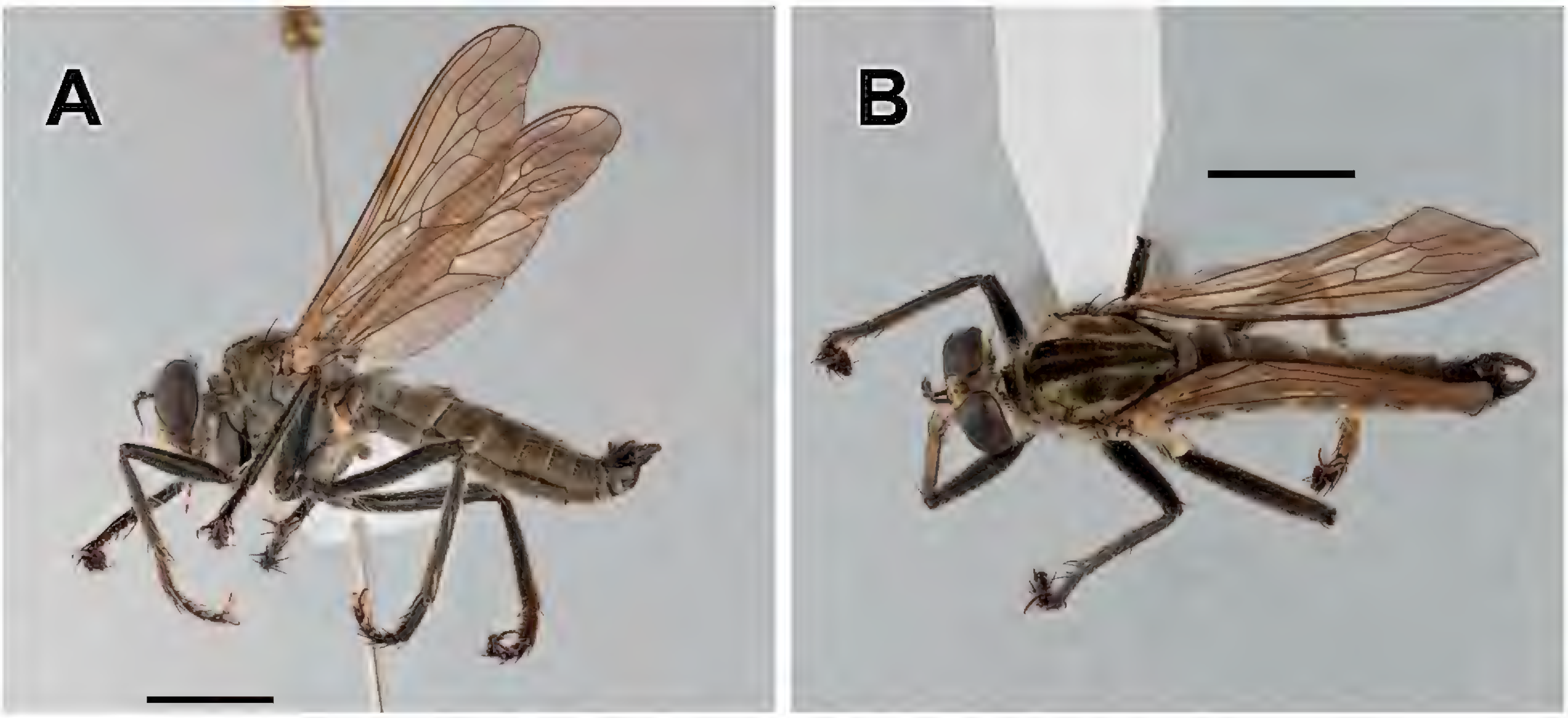

Fig. 5. *Philonicus nagatomii* Utsuki, 2008, male habitus. **A**. Lateral view. **B**. Dorsal view. Scale bars = 2 mm.

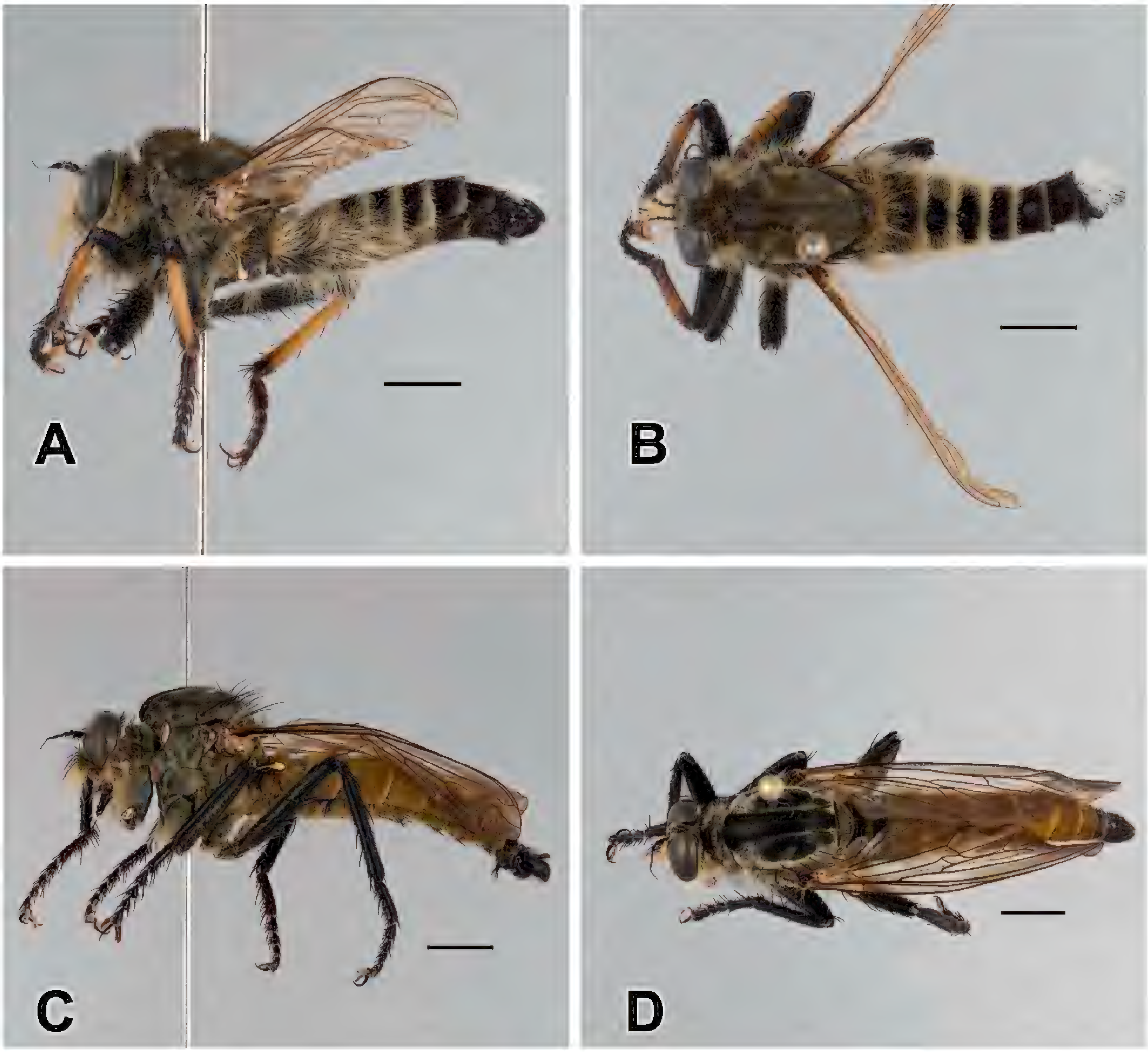

Fig. 6. A–B. *Promachus yesonicus* Bigot, 1887, male habitus. **A.** Lateral view. **B**. Dorsal view. **C–D**. *Trichomachimus scutellaris* (Coquillett, 1989), male habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

23 Aug.–2 Sep. 2014 (1); Fukuoka Pref., Fukuoka, Nogochi: 17 Aug. 1997 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu; Korean Peninsula.

Trichomachimus Engel, 1934
Trichomachimus scutellaris (Coquillett, 1989)
Fig. 6C–D
Asilus scutellaris Coquillett, 1898. Proc. U.S. Natl. Mus. 21: 315 – Type locality: "Japan" – Type collection: USNM [SD].

References for identification. Tagawa (1981), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 05–19 Jul. 2014 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu; Russian Far East; China.

Brachyrhopalinae

Cyrtopogon Loew, 1847
Cyrtopogon pictipennis Coquillett, 1898
Fig. 7A–B
Cyrtopogon pictipennis Coquillett, 1898. Proc. U.S. Natl. Mus. 21: 311 – Type locality: Japan – Type collection: USNM [SD].

References for identification. Tagawa (2001).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 24–31 May 2015 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 21–29 Jun. 2014 (2).

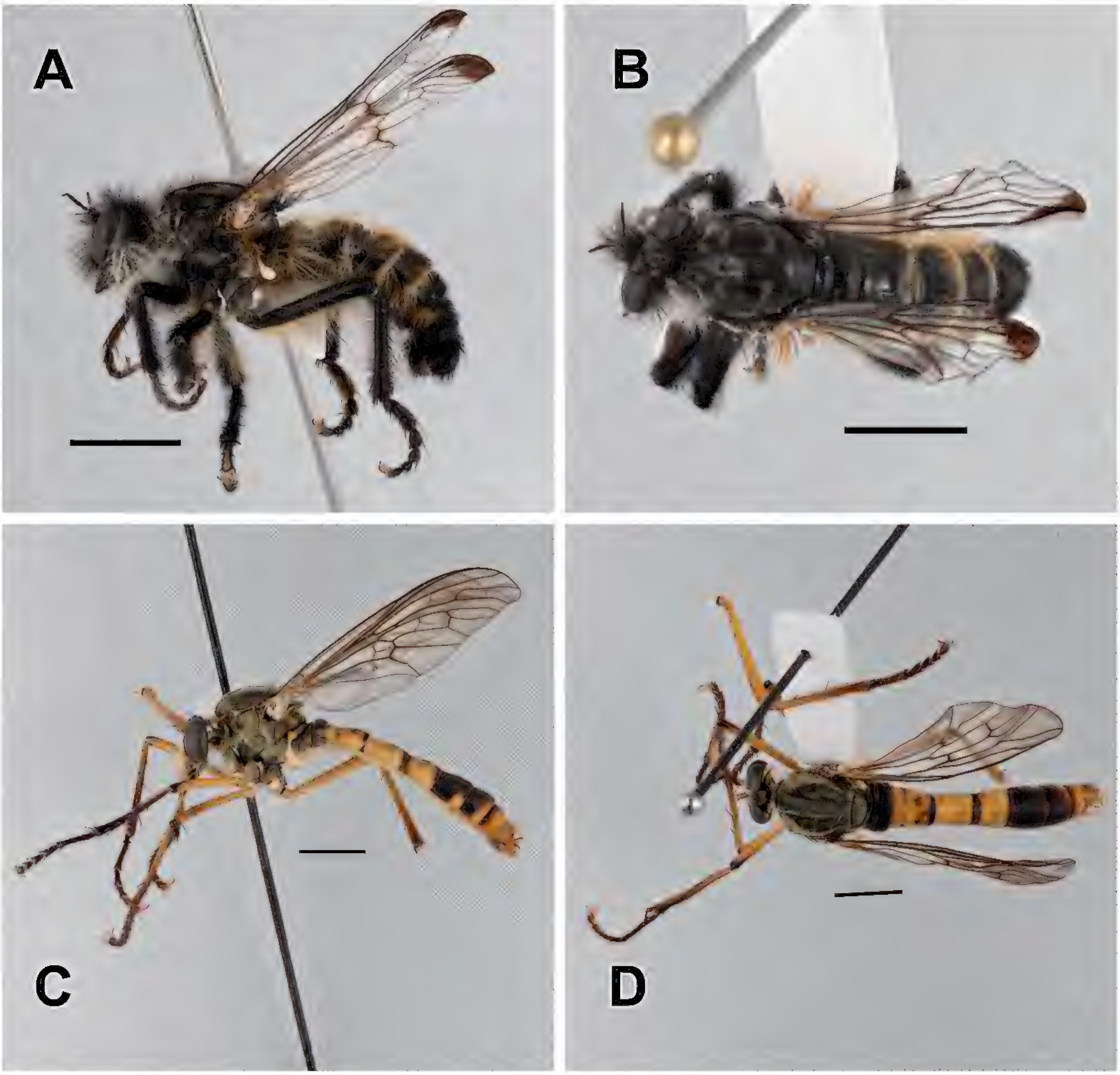

Fig. 7. A–B. *Cyrtopogon pictipennis* Coquillett, 1898, male habitus. **A**. Lateral view. **B**. Dorsal view. **C–D**. *Molobratia sapporensis* (Matsumura, 1916), male habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

Distribution. Japan: Honshu, Shikoku, Kyushu.

Dasypogoninae

Molobratia Hull, 1958
Molobratia sapporensis (Matsumura, 1916)
Fig. 7C–D
Dasypogon sapporensis Matsumura, 1916. Thous. Ins. Jpn. Vol. 2: 289 – Type locality: Japan: Hokkaido – Type collection: EIHU [GG].

References for identification. Nagatomi et al. (1989).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (8); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (7); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (43); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (43): Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 2–11 Aug. 2014 (5); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 11–23 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 11–23 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 23 Aug.–2 Sep. 2014 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu.

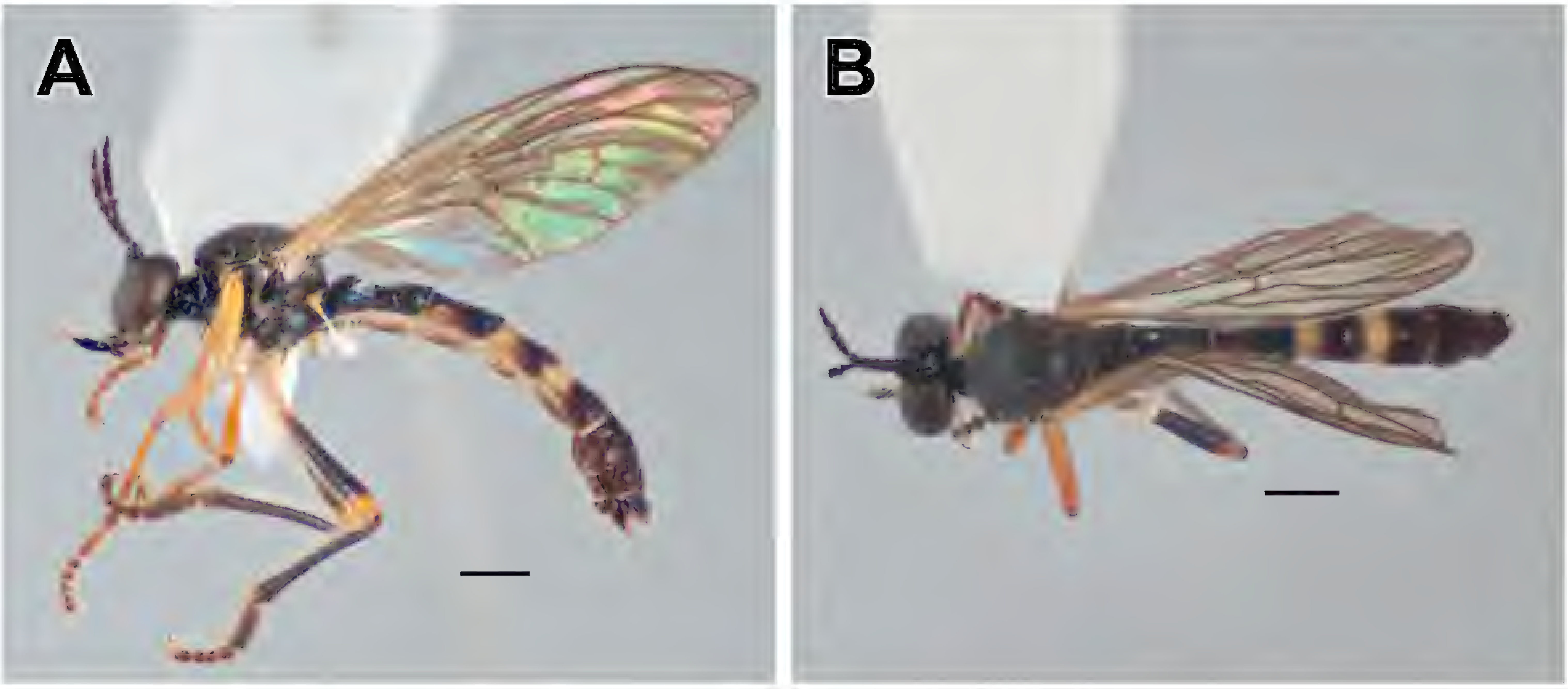

Fig. 8. *Dioctria nakanensis* Matsumura, 1916, male habitus. **A**. Lateral view. **B**. Dorsal view. Scale bars = 1 mm.

Dioctriinae

Dioctria Meigen, 1803
Dioctria nakanensis Matsumura, 1916
Fig. 8A–B
Dioctria nakanensis Matsumura, 1916. Thous. Ins. Jpn. Vol. 2: 294 – Type locality: Japan: Honshu & Kyushu – Type collection: EIHU [GG].

References for identification. Lehr (2002), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (2); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (5); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (12); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 2–11 Aug. 2014 (4); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 23 Aug.–2 Sep. 2014 (1).

Distribution. Japan: Honshu, Shikoku, Kyushu; Taiwan.

Laphriinae

***Choerades* Walker, 1851**
Choerades komurae (Matsumura, 1911)
Fig. 9A–B
Laphria komurae Matsumura, 1911. J. Fac. Agric. Hokkaido Univ. 4: 70 – Type locality: “Kusunnai” [= Iljinskiy, Sakhalin] (Russia) – Type collection: EIHU [GG].
Choerades lubarskii Esipenko, 1969. Uchen. Zap. Khabarovsk, gos. pedagog. Inst. 18: 63. Type locality: Sakhalin, Novo-Aleksandrovsk (Russia).

References for identification. Hua (1989), Young & Hradský (2007), Tagawa (2020).

New records. Fukuoka Pref., Fukuoka, Nogochi: 07 Jun. 1997 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (3).

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu; Russia: Kuril Island, Sakhalin.

Choerades sp.
Fig. 9C–D

References for identification. Hua (1989), Young & Hradský (2007), Tagawa (2020).

Records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (1).

Distribution. Tagawa (2020) records this unnamed taxon from Honshu and Shikoku.

Remarks. Our specimen belongs to the species named “*Choerades* sp.2” in Tagawa (2020). According to Tagawa (personal communication), this taxon is a new species that he plans to describe.

Laphria Meigen, 1806
Laphria rufa Röder, 1887
Fig. 10A–D
Laphria rufa Röder, 1887. Mitt. Schweiz. entomol. Ges. 7: 192 – Type locality: “Japan” – Type collection: unknown.

References for identification. Hua (1989), Young & Hradský (2007), Tagawa (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (3); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (2); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 19 Jul.–2 Aug. 2014 (1).

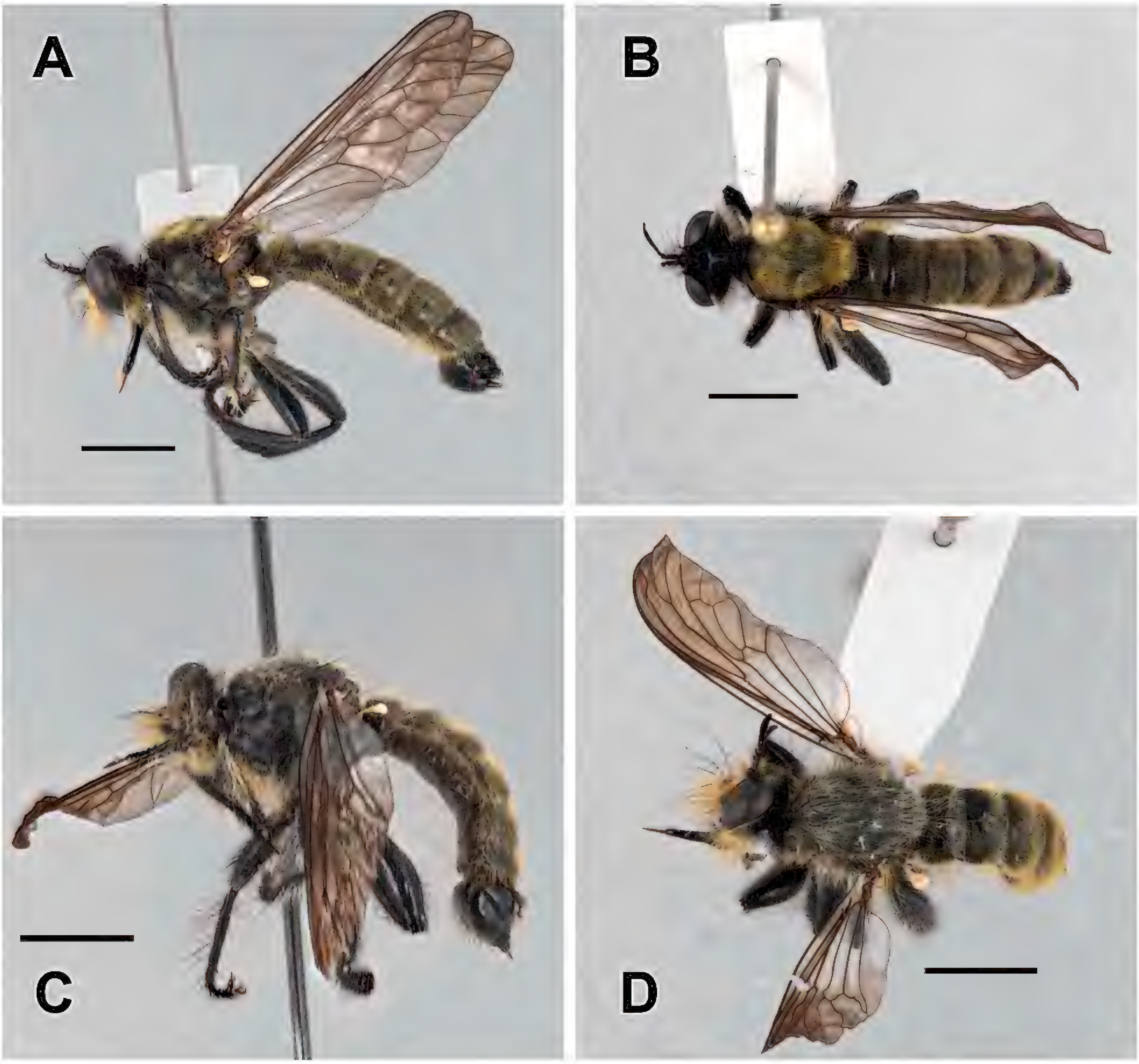

Fig. 9. A–B. *Choerades komurae* (Matsumura, 1911), male habitus. **A.** Lateral view. **B**. Dorsal view. **C–D**. *Choerades* sp., male habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu; Russia: Kuril Islands, Sakhalin; China.

Remarks. Species very similar to *Laphria mitsukurii* Coquillet, 1898. According to Young & Hradský (2007), *L. rufa* has yellow hairs on mesoscutum posterior to the scutellar suture, yellow hairs on tergites 1–3 and long mats of yellow hairs on tergites 4–6; whereas *L. mitsukurii* has black hairs posterior to the scutellar suture, black hairs on tergites 1–3 and long mats of orange hairs on tergites 5–6. Some of our specimens are somewhat intermediate in having yellow to orange hairs on the posterior mesoscutum but black hairs on tergites 1-3 and orange hairs on tergites 4–6 (compare Fig. 3A–B to Fig. 3C–D). Our identification as *L. rufa* is justified by the presence of yellowish hair on the posterior mesoscutum. Young & Hradský (2007) stated that. "The two species (*L. mitsukurri* and *L. rufa*) are, in their numerous variations, externally different, but uncharacteristically for asilids, the males show almost identical features in the internal structures of the genitalia (gonopod, gonostylus, gonocoxite)". Hence, further investigations on the morphological and/or molecular separation of the two species seem necessary.

Maira Schiner 1866
Maira aterrima Hermann, 1914
Fig. 10E–F

Maira aterrima Hermann, 1914. Entomol. Mitt. 3: 110 – Type locality: China: Guangdong, Guangzhou [= Canton]; Taiwan: Taihorinsho – Type collection: unknown.

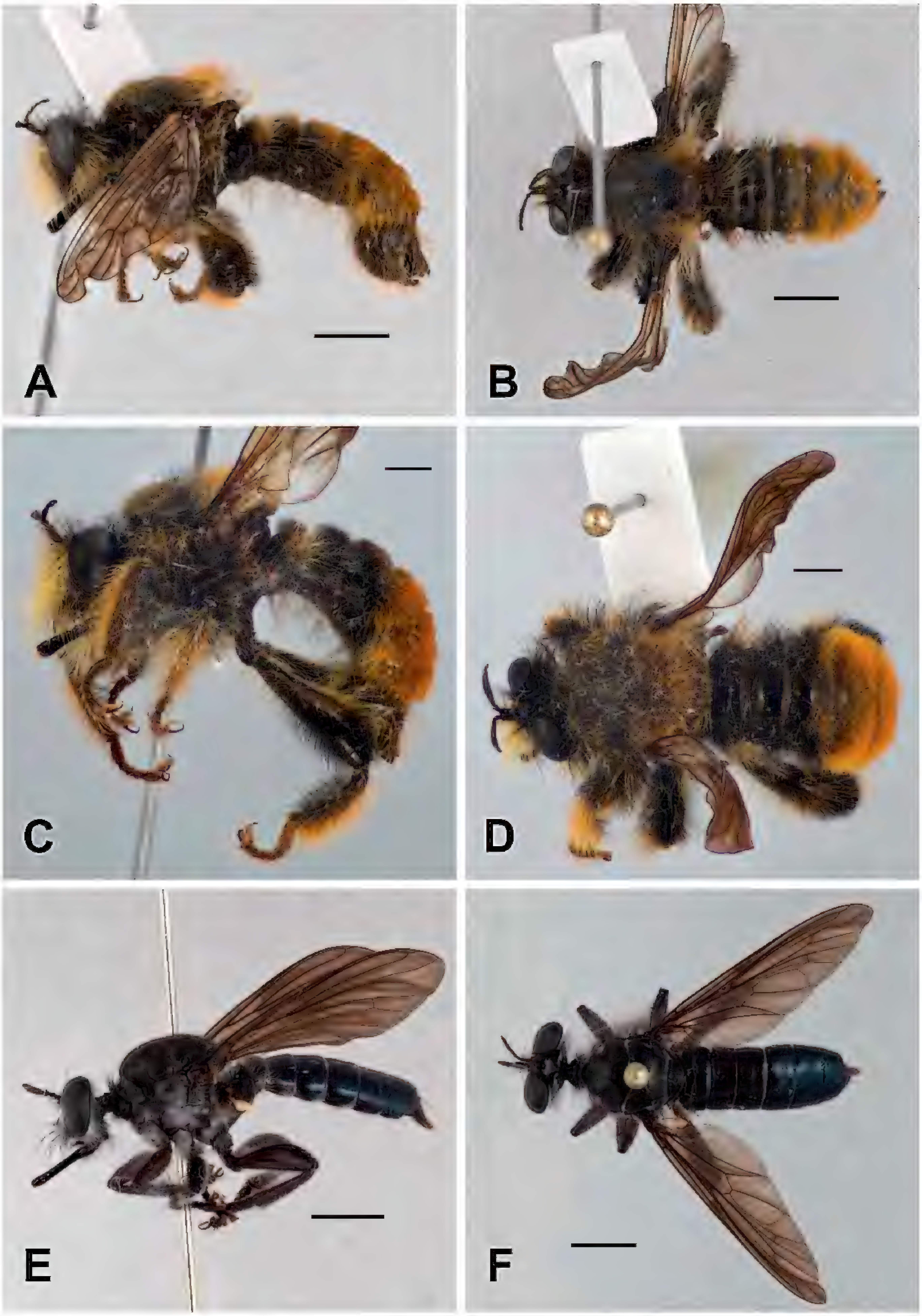

Fig. 10. A–D. *Laphria rufa* Röder, 1887, male habitus. **A**. Lateral view of a light-coloured male. **B**. Dorsal view of a light-coloured male. **C**. Lateral view of a dark-coloured male. **D**. Dorsal view of a dark-coloured male. **E–F**. *Maira aterrima* Hermann, 1914, female habitus. **E**. Lateral view. **F**. Dorsal view. Scale bars: A–B, E–F = 2 mm; C–D = 1 mm.

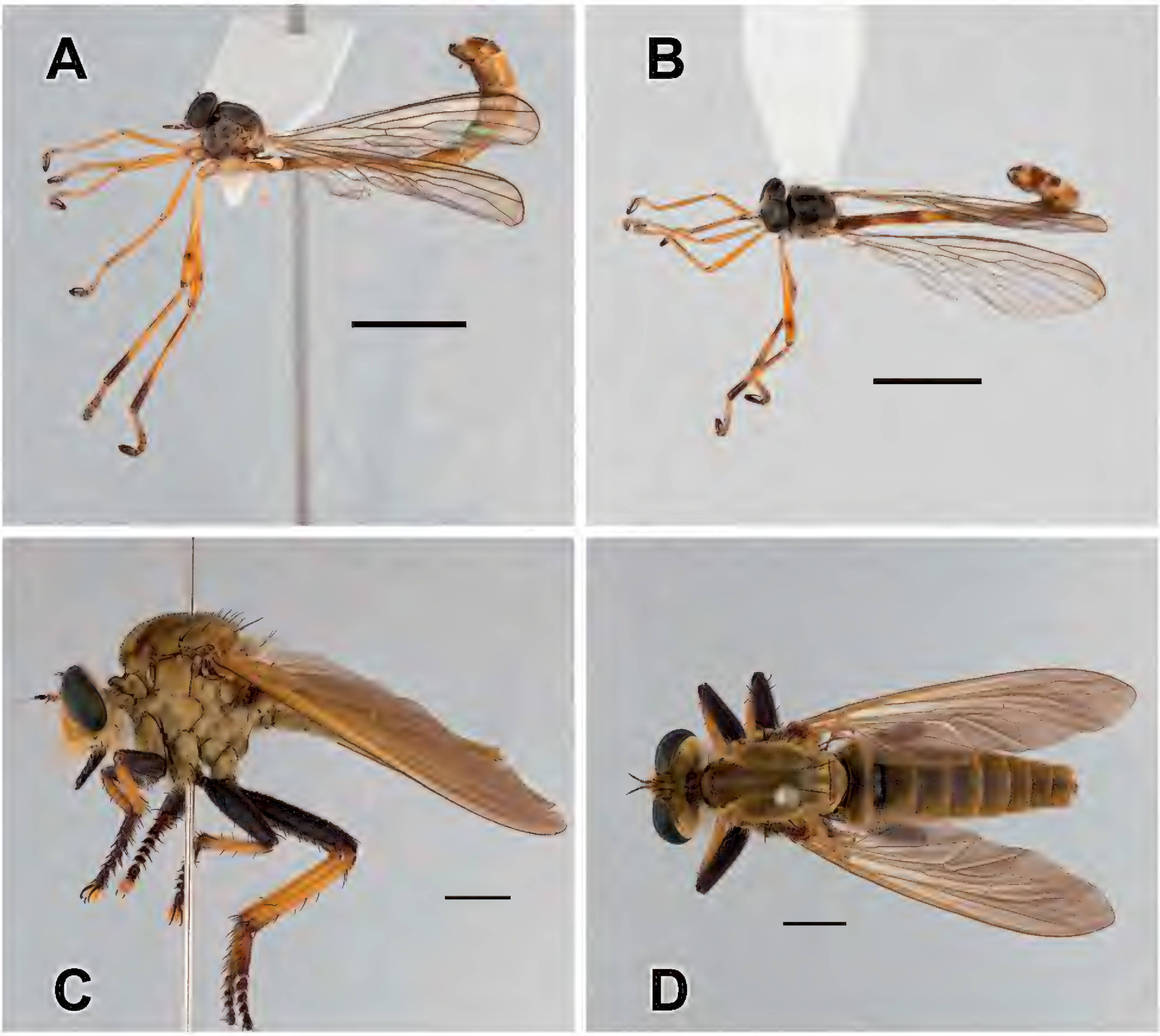

Fig. 11. A–D. *Leptogaster humeralis* (Hsia, 1949), male habitus. **A**. Lateral view. **B**. Dorsal view. **C–D**. *Cophinopoda chinensis* (Fabricius, 1794), female habitus. **C**. Lateral view. **D**. Dorsal view. Scale bars = 2 mm.

References for identification. Hermann (1914), Hua (1986), Weinberg & Parvu (1999), Young & Hradský (2007).

New records. Okinawa, Hiji Falls: 11 May 1999 (1).

Distribution. Japan: Kyushu, Ryukyu Islands; Taiwan; China.

Remarks. Not listed in Lehr (1988).

Leptogastrinae

Leptogaster Meigen, 1803
Leptogaster humeralis (Hsia, 1949)
Fig. 11A–B
Psilonyx humeralis Hsia, 1949. Sinensia 19: 25 294 – Type locality: China: Zhejiang, Tienmushan – Type collection: unknown.

References for identification. Lehr (1961), Kuroda (2020).

New records. Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 29 Jun.–5 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 5–19 Jul. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 19 Jul.–2 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 2–11 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, forest (B2): 2–11 Aug. 2014 (1); Nagano Pref., Ueda, Sugadaira Research Station, grassland (B1): 11–23 Aug. 2014 (1), Kumamoto Pref., Izumi-mura, Siibagoe: 24 Aug. 1997 (1).

Distribution. Japan: Hokkaido, Honshu, Shikoku; Russia: Primorsky Krai; China: Zhejiang Province.

Ommatiinae

***Cophinopoda** Hull*, 1958

Cophinopoda chinensis (Fabricius, 1794)

Fig. 11C–D

Asilus chinensis Fabricius, 1794. Entomol. syst. Tome IV: 383 – Type locality: "China" – Type collection: ZMUC [SD].

Dasypogon flavescens Fabricius, 1805. Syst. Antl.: 169 – Type locality: Indonesia: Sumatra – Type collection: ZMUC [SD].

Ommatius fulvidus Wiedemann, 1821. Dipt. exot. [Ed.2] Pars I: 214 – Type-locality: Indonesia: Java – Type collection: ZMUC [SD].

Ommatius coryphe Walker, 1849. List Dipt. Brit. Mus., part 2: 469 – Type locality: not given – Type collection: BMNH [SD].

Ommatius chinensis: Matsumura (1931): Illustr. ins. Japan: 325.

References for identification. Tsacas & Artigas (1994).

New records. Fukuoka Pref., Fukuoka, Chayama: 20 Jun. 1999 (1); Fukuoka Pref., Fukuoka, Chayama: 16 Jul. 1999 (1).

Distribution. Japan: Honshu; India; Sri Lanka; China; Vietnam; Java; Sumatra.

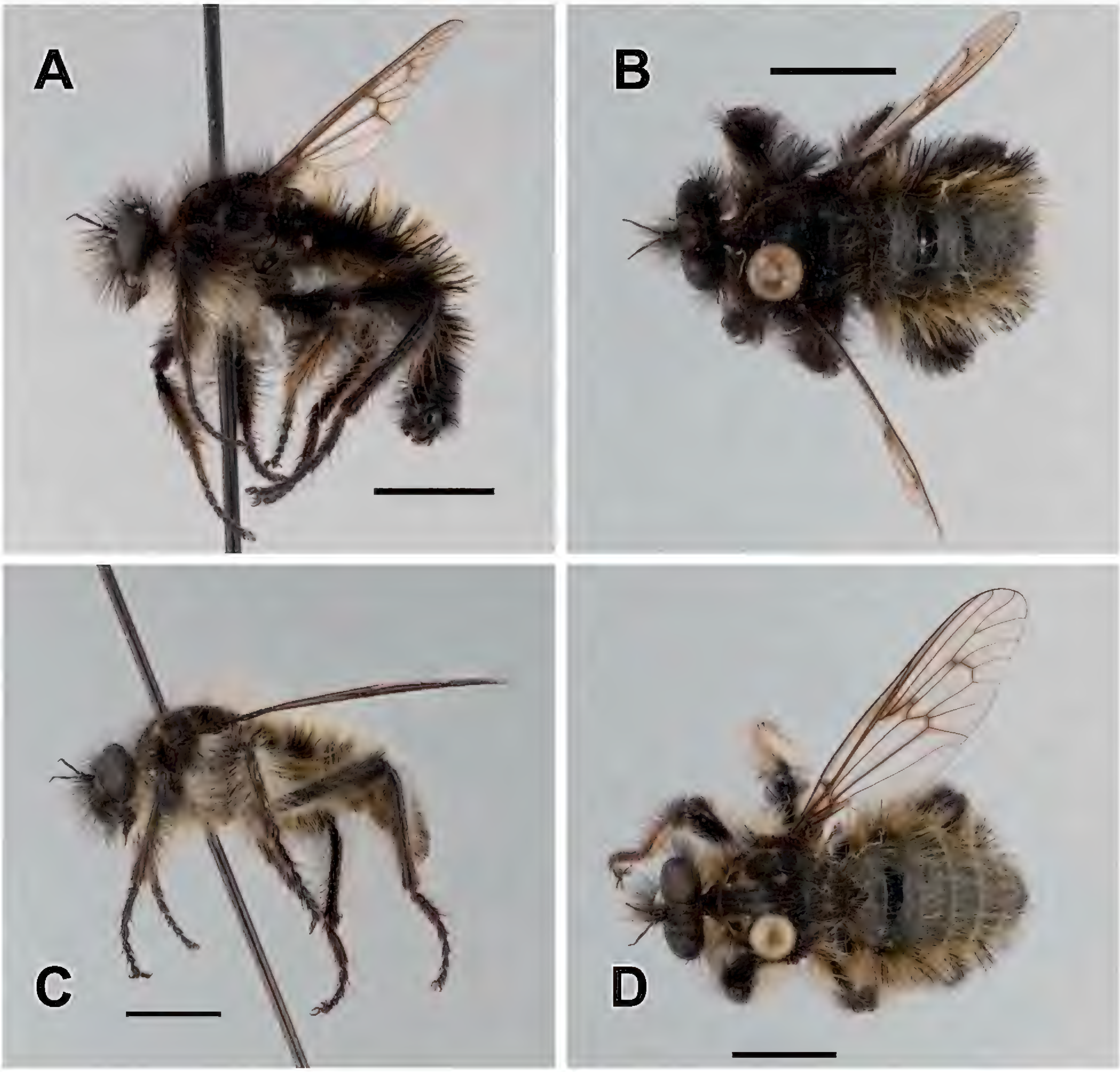

Fig. 12. *Grypoctonus aino* Speiser, 1928. **A–B**. Male habitus. **A**. Lateral view. **B**. Dorsal view. **C–D**. Female habitus. Scale bars = 2 mm.

Remarks. According to Tsacas & Artigas (1994), *C. chinensis* and *C. oldroydi* have very similar female genitalia. Their key mentions the structure of sternite VIII to distinguish both. Our specimens clearly key to *C. chinensis* and lack the patch of black bristles on sternite III mentioned in the description of *C. oldroydi* and not mentioned in the redescription of the female holotype of *C. chinensis*. Tsacas & Artigas (1994) described *C. oldroydi* from Japan and recorded *C. chinensis* from the Asian mainland. However, according to Tagawa (2020) the separation of both species is doubtful.

Stenopogoninae

Grypoctonus Speiser, 1928
Grypoctonus aino Speiser, 1928
Fig. 12A–D
Grypoctonus aino Speiser, 1928. Schr. phys.-okon. Ges. Konigsberg 65: 156 – Type locality: Japan: Nagasaki – Type collection: ZSMC [Hradský & Geller-Grimm (1999)].

References for identification. Hradský & Geller-Grimm (1999), Tagawa (2020).

New records. Fukuoka Pref., Mount Sefuri: 25 Oct. 1997 (4).

Distribution. Japan: Honshu, Shikoku, Kyushu.

Remarks. Lehr (1988) listed *G. aino* as synonym of *Grypoctonus hatakeyamae* (Matsumura, 1916), but Hradský & Geller-Grimm (1999) studied the types of Speiser and concluded that *G. aino* is a valid species based on the wing venation and the morphology of the male genitalia.

Stichopogoninae

Stichopogon Loew, 1847
Stichopogon gracilifemur **Nagatomi, 1983**
Fig. 13A–B
Stichopogon gracilifemur Nagatomi, 1983. Kontyû 51: 476 – Type locality: Japan: Nagano Pref., Takato – Type collection: unknown [Nagatomi (1983) stated that the holotype was temporarily deposited at the Faculty of Agriculture, Kagoshima University, Kagoshima, Japan].

References for identification. Nagatomi (1983), Tagawa (2020).

New records. Kumamoto Pref., Itsuki-mura: 25 Aug. 1998 (5).

Distribution. Japan: Honshu, Kyushu.

Remarks. These are the first distribution records of this species for Kyushu.

DISCUSSION

All reported species here were already listed for Japan by Utsuki (2014). Nevertheless, we provide the first published records of *Stichopogon gracilifemur* Nagatomi, 1983 from Kyushu. The majority of our studied material was collected by Malaise traps at the Sugadaira Research Station, where 16 species were collected. The relatively high species number despite the low spatial coverage is probably best explained by the high habitat diversity at Sugadaira-Kogen as well as the relatively high sampling effort (two years of Malaise trap sampling during the flight season, yielding 314 specimens). In contrast, the

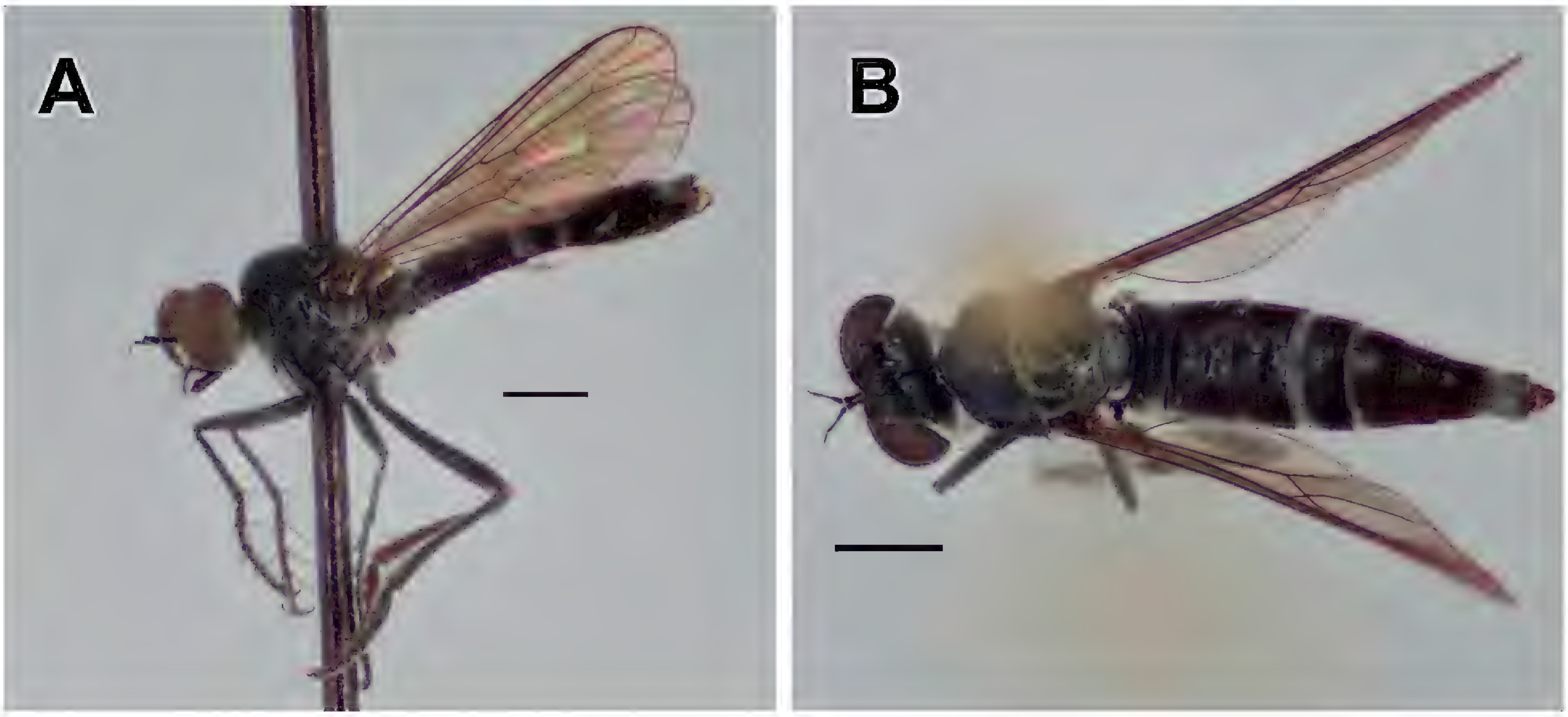

Fig. 13. *Stichopogon gracilifemur* Nagatomi, 1983, female habitus. **A**. Lateral view. **B**. Dorsal view. Scale bars = 1 mm.

material collected by hand-net has a greater spatial coverage (eight sites from Kyushu, one from Okinawa). The fact that no robber fly was sampled in 2016 is probably due to the timing. Firstly, the traps were set up only for eight days and, secondly, the traps were set quite early in the year.

At least since the work of Shōnen Matsumura in the early 20th century, asilidology is an established research field in Japan. Hence, the Japanese asilid fauna can be considered fairly well researched. Yet, there are still some challenges to overcome. Although there is detailed and illustrated literature for most species that occur in Japan, many publications are older than 40 years or focus on different geographical regions than Japan and a comprehensive key is only present for a handful of genera. We hope that our work, presenting high quality images and detailed information on synonymy, distribution and literature contributes to increase the accessibility of the Japanese Asilidae fauna for future studies.

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APPENDIX I

(*electronic supplement, available at www.zoologicalbulletin.de*)

Table S1. Systematic and identification data for the specimens studied in the present work.

BHL

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Appendix 1. Systematic and identification data for the specimens studied in the

Family	Genus Name	Species Name	Author	Date description
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Choerades	sp.		
Asilidae	Cyrtopogon	pictipennis	Coquillett	1898
Asilidae	Cyrtopogon	pictipennis	Coquillett	1898
Asilidae	Cyrtopogon	pictipennis	Coquillett	1898
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
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Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Dioctria	nakanensis	Matsumura	1916
Asilidae	Eutolmus	brevistylus	Coquillett	1898
Asilidae	Eutolmus	brevistylus	Coquillett	1898
Asilidae	Eutolmus	brevistylus	Coquillett	1898
Asilidae	Eutolmus	brevistylus	Coquillett	1898
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Asilidae	Eutolmus	brevistylus	Coquillett	1898
Asilidae	Eutolmus	brevistylus	Coquillett	1898
Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
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Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
Asilidae	Eutolmus	koreanus	Hradský & Hüttinger	1985
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Laphria	rufa	Röder	1887
Asilidae	Trichomachimus	scutellaris	Coquillett	1898
Asilidae	Molobratia	sapporensis	Matsumura	1916

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Asilidae	Neoitamus	angusticornis	Loew	1858
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Asilidae	Neoitamus	angusticornis	Loew	1858
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Asilidae	Neoitamus	angusticornis	Loew	1858
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Asilidae	Neoitamus	angusticornis	Loew	1858
Asilidae	Neoitamus	angusticornis	Loew	1858
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
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Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	castaneipennis	Tagawa	1981
Asilidae	Neoitamus	univittatus	Loew	1871
Asilidae	Neoitamus	univittatus	Loew	1871
Asilidae	Neoitamus	univittatus	Loew	1871
Asilidae	Neoitamus	univittatus	Loew	1871
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Asilidae	Neoitamus	univittatus	Loew	1871
Asilidae	Neoitamus	ishiharai	Tagawa	1981
Asilidae	Philonicus	nagatomii	Utsuki	2008
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Choerades	komurae	Matsumura	1911
Asilidae	Cophinopoda	chinensis	Fabricius	1794
Asilidae	Cophinopoda	chinensis	Fabricius	1794
Asilidae	Grypoctonus	aino	Speiser	1928
Asilidae	Grypoctonus	aino	Speiser	1928
Asilidae	Grypoctonus	aino	Speiser	1928

Asilidae	Grypoctonus	aino	Speiser	1928
Asilidae	Maira	aterrima	Herrmann	1914
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Asilidae	Neoitamus	angusticornis	Loew	1858
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Promachus	yesonicus	Bigot	1887
Asilidae	Leptogaster	humeralis	Hsia	1949
Asilidae	Stichopogon	gracilifemur	Nagatomi	1983
Asilidae	Stichopogon	gracilifemur	Nagatomi	1983
Asilidae	Stichopogon	gracilifemur	Nagatomi	1983
Asilidae	Stichopogon	gracilifemur	Nagatomi	1983
Asilidae	Stichopogon	gracilifemur	Nagatomi	1983

present work

Brackets	Determined by	Date determination	Country	Area/State
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0	Bock, K.	2020	Japan	Kyushu, Kumamoto Prefecture
0	Bock, K.	2020	Japan	Kyushu, Kumamoto Prefecture

City	Locality	Lat	Long	Ecology	Altitude
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m

Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m

Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m

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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
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Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
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Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m

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Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m

Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52389	138,3494	Grassland	1330 m
Ueda	Sugadaira Kogen, near SMRC	36,52167	138,3508	Forest	1335 m
Fukuoka	Nogochi			Forest	260 m
Fukuoka	Chayama				
Fukuoka	Chayama				
	Mount Sefuri			Beech	1000 m
	Mount Sefuri			Beech	1000 m
	Mount Sefuri			Beech	1000 m

	Mount Sefuri	Beech	1000 m
	Hiji Falls	Hardwood forest	
	Mt. Raizan, Maebaru-shi		500-600 m
Fukuoka	Nogochi		260 m
	Shiiba-goe	Hardwood forest	1250 m
	Mt. Raizan, Maebaru-shi		500-600 m
Fukuoka	Chayama		
Fukuoka	Nogochi	Forest	260 m
	Izumi-mura, Siibagoe	Hardwood forest	1250 m
	Itsuki-mura		
	Itsuki-mura		
	Itsuki-mura		
	Itsuki-mura		
	Itsuki-mura		

Starting Day	Starting Mo	Starting Yea	Ending day	Ending Mor	Ending Yea	period of ti	Sex
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Female
29	June	2014	5	July	2014		Male
5	July	2014	19	July	2014		Female
19	July	2014	2	August	2014		Male
24	May	2014	31	May	2015		Male
21	June	2014	29	June	2014		Male
21	June	2014	29	June	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
29	June	2014	5	July	2014		Female
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Male
5	July	2014	19	July	2014		Male
5	July	2014	19	July	2014		Female
2	August	2014	11	August	2014		Female
23	August	2014	2	September	2014		Female
2	August	2014	11	August	2014		Female
2	August	2014	11	August	2014		Female
19	July	2014	2	August	2014		Male
2	August	2014	11	August	2014		Female
2	August	2014	11	August	2014		Male
2	August	2014	11	August	2014		Male
19	July	2014	2	August	2014		Male
19	July	2014	2	August	2014		Female
19	July	2014	2	August	2014		n.a.
19	July	2014	2	August	2014		Female
5	July	2014	19	July	2014		Male
29	June	2014	5	July	2014		Male
29	June	2014	5	July	2014		Male
29	June	2014	5	July	2014		Male

5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Male
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
29 June	2014	5 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
2 August	2014	11 August	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
21 June	2014	29 June	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Male
2 August	2014	11 August	2014	Female

19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
2 August	2014	11 August	2014	Male
2 August	2014	11 August	2014	Female
2 August	2014	11 August	2014	Female
2 August	2014	11 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
23 August	2014	2 September	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female

29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
11 August	2014	23 August	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Male
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Female
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male

5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Male
11 August	2014	23 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	n.a.
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
29 June	2014	5 July	2014	Male
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
19 July	2014	2 August	2014	Female
19 July	2014	2 August	2014	Male
5 July	2014	19 July	2014	Female

19 July	2014	2 August	2014	Male
19 July	2014	2 August	2014	Female
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
5 July	2014	19 July	2014	Male
5 July	2014	19 July	2014	Female
29 June	2014	5 July	2014	Female
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Male
5 July	2014	19 July	2014	Male
2 August	2014	11 August	2014	Female
5 July	2014	19 July	2014	Male
2 August	2014	11 August	2014	Female
29 June	2014	5 July	2014	Male
2 August	2014	11 August	2014	Male
2 August	2014	11 August	2014	Male
21 June	2014	29 June	2014	Female
19 July	2014	2 August	2014	Male
2 August	2014	11 August	2014	n.a.
5 July	2014	19 July	2014	Male
2 August	2014	11 August	2014	Male
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Female
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
24 May	2015	31 May	2015	Male
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Female

21 June	2014	29 June	2014	Female
17 May	2015	24 May	2015	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Male
29 June	2014	5 July	2014	Male
21 June	2014	29 June	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Female
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Male
21 June	2014	29 June	2014	Female
21 June	2014	29 June	2014	Male
29 June	2014	5 July	2014	Male
29 June	2014	5 July	2014	Male
11 August	2014	23 August	2014	Male
2 August	2014	11 August	2014	Female
2 August	2014	11 August	2014	Male
23 August	2014	2 September	2014	Male
5 July	2014	19 July	2014	Female
11 August	2014	23 August	2014	Female
11 August	2014	23 August	2014	Male
11 August	2014	23 August	2014	Male
11 August	2014	23 August	2014	Male
2 August	2014	11 August	2014	Male
19 July	2014	2 August	2014	Male
29 June	2014	5 July	2014	Female
29 June	2014	5 July	2014	Female
5 July	2014	19 July	2014	Male
11 August	2014	23 August	2014	Female
2 August	2014	11 August	2014	Female
7 June	1997			Male
16 July	1999	18 July	1999	Female
20 June	1999			Female
25 October	1997			Male
25 October	1997			Male
25 October	1997			Female

25 October	1997	Male
11 May	1999	Female
14 June	1997	Male
7 June	1997	Female
24 August	1997	Male
14 June	1997	Female
20 June	1999	Male
17 August	1997	Female
24 August	1997	Male
25 August	1997	Female
25 August	1997	Female
25 August	1997	Female
25 August	1997	Female
25 August	1997	Female

Collector	Specimens	Notes	Unique Identifier
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052634
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052648
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052653
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052700
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053238
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053147
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052679
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00053249
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00053254
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052631
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052636
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052637
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052638
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052639
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052641
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052642
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052649
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052651
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00095081
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052652
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052674
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052696
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052701
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052719
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052743
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052746
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053255
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053280
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077606
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077610
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077612
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077607
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077609
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077608
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052517
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052518
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052655
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052656
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052657
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052667
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052670
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052703
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052704
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052706

Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053172
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053173
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053176
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053177
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053178
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053179
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053190
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053227
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053257
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053264
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053265
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053266
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077611
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052516
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052632
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052643
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052646
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052695
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052709
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052738
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052742
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053152
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053153
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053156
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053158
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053205
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053220
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053235
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00053234
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053259
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077605
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077603
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077604
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077600
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077601
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077602
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077599
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077598
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052654
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052665
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053187
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00012549
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00012500
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053278
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00053275
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052513

Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052659
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052661
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052739
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053174
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053268
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077646
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052510
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052511
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052512
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052635
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052658
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052662
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052663
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052684
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052691
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052692
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052693
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052707
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052711
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052712
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052713
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052714
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052732
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052733
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052734
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052735
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052736
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052737
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052740
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053160
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053161
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053162
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053163
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053164
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053165
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053166
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053167
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053168
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053169
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053170
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053171
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053175
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053186
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053191
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053201
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053203

Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053207
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053208
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053222
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053223
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053224
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053225
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053226
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053229
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053231
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053233
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053236
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053237
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053239
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053240
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053241
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053258
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00053261
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053262
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053263
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077657
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077651
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077650
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077653
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077654
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077648
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077649
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077658
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077652
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077656
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00077659
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077655
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077640
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077638
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077637
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077636
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077642
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077643
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053267
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077641
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077639
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077645
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077633
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077623
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077620
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077619
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077617

Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077634
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077647
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077621
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077630
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077627
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077635
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077629
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077625
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053626
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077632
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077618
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077615
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077624
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077616
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077628
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077622
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00077631
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052629
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052633
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052640
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052645
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052647
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052650
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052668
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052669
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052673
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052688
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052689
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052697
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052699
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052702
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052705
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052710
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052715
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052716
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052720
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052721
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052724
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052726
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052727
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052728
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052730
Blanke, A.	1	Malaise trap; Coordinates: 36°31'18"N 13	ZFMK-DIP-00052731
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052741
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00052745
Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053154

Blanke, A.	1	Malaise trap; Coordinates:36°31'26"N 13	ZFMK-DIP-00053155
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Putting the cart before the horse: taxonomy of the species of *Philopterus* (Phthiraptera: Ischnocera: Philopteridae) of the goldcrest, *Regulus regulus* (Linnaeus, 1758) (Aves: Passeriformes: Regulidae)

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Abstract. The concept of "type host" denotes the host with which the holotype (or equivalent) of a parasitic species was associated at the time of collection. This concept is often erroneously conflated with the concept of a "natural host(s)", which refers to the host(s) with which the parasite species is naturally and normally associated in the wild. In cases where these two concepts are not kept apart, and when parasites like lice (Phthiraptera) are believed to be strictly host specific, a culture of identification by host association may develop. Here, I look at the consequences of such a case, the recent rejection of *Philopterus reguli* Denny, 1842 as the valid name of the louse species that normally parasitizes *Regulus regulus* (Linnaeus, 1758), and the erection of a new name for this taxon, which was subsequently synonymized with the new name based on a proposed neotype for *Ph. reguli*. I discuss the history of *Philopterus reguli*, the known specimens of this species, and the present controversy, as well as the validity of the neotype designation. In conclusion, the neotype designation of *Ph. reguli* is rejected, as it has not been shown that the syntype is unidentifiable, suspicious, or otherwise invalid, and a change in nomenclature has not been shown to be a problem for the stability of taxonomy. Moreover, the neotype designation is invalidated by at least three separate violations of the International Code of Zoological Nomenclature. I call for more care in both specimen identification and louse taxonomy and open up for a discussion about how the louse research community can move forward together on the issue of poorly described species.

Key words. Type host, natural host, Phthiraptera, *Philopterus*, neotype designation.

CHEWING LICE

Chewing lice (Phthiraptera) are small, wingless parasites of birds and mammals. In general, chewing lice do not easily spread between hosts except when two hosts come into physical contact, but many exceptions are known (e.g., Gustafsson & Najer 2022). Moreover, lice lack free-living life stages, and the host's feathers or fur serve as both habitat, egg-laying surface, and food for lice. As a result, lice have evolved to be exceptionally dependent on their hosts, making them excellent model systems for, for example, research into co-evolution (Clayton et al. 2016).

However, research on lice is often hampered by difficulties in identifying lice, sometimes even to genus level. This is partially due to the relatively little attention lice have received in the last century, compared to larger and more easily collected insect groups. For instance, there were no general checklists with illustrations of all different genera until Price et al. (2003), there are almost no national or regional checklists of lice (but see, e.g., Ilieva 2009; Palma 2017; Oslejskova et al. 2021), and no general genus-level key to the largest group of lice, the Ischnocera, has ever been published. In addition to this lack of resources, the most significant obstacle to louse identification is the generally poor descriptions and illustrations provided for a large proportion of the known lice. At least partially, this is due to an overreliance on host associations over louse morphology by many of the most prolific louse taxonomists throughout the 20th century. Here, I examine a recent case in louse taxonomy that highlights the shortcomings of this approach.

THE REVERSE OF HELPFUL

The concept of the "type host" of chewing lice has accrued an undeserved and irrational importance in chewing louse taxonomy over the last century. If a host species has been designated the type host of a louse species, then any congeneric louse specimens on the same host species have sometimes been assumed to be conspecific with the known louse species. Conversely, if a louse specimen is found on a host that has not previously been designated

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the type host of any louse of that genus, this has been seen as sufficient evidence that this specimen must be novel.

Examples of this are numerous throughout the published louse literature, although some are more egregious than others: Eichler (1950) described two new subspecies of *Auricotes* Kéler, 1940, based on specimens he himself had not studied, but which were discussed by Kéler (1940). In both cases, Kéler (1940) mentioned that specimens from some non-type hosts deviated slightly from specimens from type hosts, but no details were given, and Kéler considered the specimens he had examined to be too few to draw any conclusions. No morphological argument for their division was thus ever published by Kéler (1940), nor did Eichler (1950) add any morphological detail. It seems reasonable to consider these names to be in violation of Article 13.1.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999; hereafter: the Code), and thus unavailable. Hopkins & Clay (1953: 443) chided Eichler for exactly this behaviour, and memorably called it "the reverse of helpful".

Similarly, Złotorzycka (1964a, b) made a habit of separating species she had not examined based on the family-level classification of their hosts. She also in many cases restricted or fixed type hosts of species she had not examined, but which were described as occurring on more than one host species, then declared that lice living on the other listed host were "most probably some other not yet described species". Typically, she then removed the non-type hosts from the lists of host associations of the lice, thus asserting that the observations of other researchers are invalid, without ever having seen any of the specimens in question. Gustafsson & Najer (2022) recently discussed many other similar examples.

More generally, checklists and revisions typically explicitly separate type hosts from other hosts or denote which host species in a list of known species is the type host (e.g., Price et al. 2003; Gustafsson & Bush 2017). However, from a broadly biological point of view, type host information is irrelevant. The type host is nothing more than the identity of the host individual the louse specimen designated as the holotype (or equivalent) was associated with at the time of collection (cf. the 'Glossary" of the Code). That is, the information conveyed by stating the type host of a louse species is that at least once, this louse species was associated with this host species. It does not, strictly speaking, imply that there will be any future records of associations between these two taxa.

In contrast, the biologically relevant term is the "natural host" (cf. Palma 2015), which may be defined generally as the host species (or set of host species) on which there is reason (based on some criteria) to believe that the vast majority of the world population of a louse species can be found under non-artificial circumstances. This concept conveys a very different kind of information, as a "natural host" designation is the assertion that this louse species could in theory be found on other specimens of this host in the future.

The type host and the natural host may be the same but may also be different. The louse literature is replete with taxa described from hosts later considered to be non-natural (e.g., Palma 1994, 2005; Adams et al. 2005; Gustafsson et al. 2019a). Recently, a new family of amblyceran lice was even proposed based on specimens from an unknown host that could not be determined even to class level [bird or mammal; Mey (2019)]. The only way to ascertain whether the type host is also the natural host is to examine more conspecific hosts and establish (to some satisfactory level of regularity) that lice from this host species are habitually conspecific with a given louse holotype.

Moreover, in my opinion, knowledge of the type host of is largely irrelevant even from a taxonomic point of view. Classification of organisms should be based on data derived from intrinsic characters of the organisms examined, not from extrinsic circumstances of their collection. From a strictly taxonomic point of view, there is no clear difference between stating "these two lice were both collected from the same host species, therefore they are conspecific" and saying, "these two lice were both collected on June 26th, therefore they are conspecific". In both cases, only intrinsic characters (e.g., morphology, genetics) of the specimens can determine if the statements are correct. "Type host", in contrast, is an extrinsic character that is irrelevant to the classification of the louse taxon.

Similarly, species identity and species limits cannot be ascertained by type host data alone; they require intrinsic data from the species in question. Arguments of identification that center on host identity are by definition spurious, and relevant only if the holotype (or equivalent) is known to be lost or ambiguous, and there is reason to clarify the identity of a taxon name by designating a neotype. In those cases, the type host serves much the same purpose as a type locality for free-living organisms, and neotypes from the same host should be ideally selected to increase the likelihood that the old types and the new types are conspecific (cf. Recommendation 75A of the Code). Crucially, these neotypes should then also be selected from a geographically similar location to the old types, given that there may be geographical variation in the lice as well as their hosts (e.g., Escalante et al.2016).

Although no overview of this development has been published, it seems reasonable to assume that at least part of this obsession with type hosts stems from the widespread belief of many earlier authors that louse data could assist in establishing relationships between hosts in cases where the data from the hosts were inconclusive (e.g., Clay 1950). This was assumed because 1) lice were believed to evolve slower than their hosts and thus could retain phylogenetic information that had been lost in their hosts through, for example, convergence, and 2) host switching was believed to be rare. Type hosts could then be used as the hooks on which to hang hypotheses of host associations, but that required the assumption that type hosts and natural hosts are the same. If they are, and the two assumptions mentioned above are valid, then two closely related louse species implicitly must have type hosts that are closely related. Seen in this light, the focus on the type host at the expense of the natural host becomes more understandable, but it does not make this shift in focus correct.

In fact, combined with the "Eichlerian methodology" (sensu Gustafsson & Najer 2022), according to which lice are considered strictly host specific and invariably following Fahrenholz's rule (Eichler 1940), the focus on type hosts rather than natural hosts may blind researchers to more interesting questions in evolutionary biology and biogeography. For instance, Eichler insisted that it is "methodologically more appropriate to say that 'we cannot yet tell two parasites from different hosts apart' than 'this parasite occurs on both these different hosts'" (Eichler 1940: 256), and that "a future review may nevertheless prove that there are morphological differences" (Eichler 1980: 412) as responses to assertions of multi-host parasites. This line of argument is intentionally blinding oneself to the possibility that lice vary in their level of host specialization, and that important general principles of louse biology may be behind this variation.

Recent research into phoresy of lice on hippoboscid flies resulting in the erosion of genetic variation among lice (DiBlasi et al. 2018) and the establishment of vast networks of host-louse associations that may span different families of hosts on different continents (e.g., Bush et al. 2016; Lee et al. 2022) has revealed a more accurate picture of louse biology. Similarly, host generalists have repeatedly been shown to exist through genetic analyses, and often be closely related to host specialists (e.g., Martinů et al. 2015; Bush et al. 2016). In other cases, host associations and species-level evolution of lice appear to be influenced by biogeography (e.g., Escalante et al. 2016) or macroevolutionary events in the history of their hosts (e.g., Boyd et al. 2022). These lines of research are possible because the bias of strict host-specificity has been removed, and collectively they reveal a much more interesting louse biology. This research has also established a more appealing worldview in which lice are not the flotsam of host evolution, but active agents to some extent responsible for their own evolutionary fate. Somewhat belatedly, lice are entering the set of organisms that may be suspected of having behaviours more sophisticated than eating, reproducing, and dying.

Nevertheless, type host designations, and discussions of type hosts, are prevalent in the chewing louse literature, and the roots may be too deep to do away with the concept altogether. Moreover, as the type host concept has some use under more strictly taxonomic circumstances, there is a need to retain the concept. However, it is important to keep in mind that the host associations – or lack thereof – of the name-bearing type specimen(s) have no bearing on the validity of the name, nor do they restrict the natural hosts of the species denoted by the name. The sooner the chewing louse community can extract itself from the obsession with type hosts, the sooner we can collectively progress to a state where louse biology and classification can be established based on data derived from the lice themselves, rather than from preconceived scenarios that may not fit the data.

To exemplify the problems that arise when type hosts and natural hosts are conflated, we will look at the species *Philopterus reguli* Denny, 1842. This will hopefully show that it is necessary to establish identity and species limits in lice based on characters of the lice themselves, and not circumstances of their collection. We will then assess the validity of recent nomenclatorial decisions made for this taxon, and finally make some general recommendations on how to approach louse identification in the future.

THE CASE OF *PHILOPTERUS REGULI* (DENNY, 1842)

Two publications during 2020 discussed the identity of *Philopterus reguli* Denny, 1842 (Najer et al. 2020; Mey 2020), a rarely reported species of head louse. Its type host is *Regulus regulus* (Linnaeus, 1758). These two publications reached complete opposite conclusions based largely on the same data. The history of the name *Philopterus reguli* can briefly be summarized as follows:

Denny (1842: 45, 91) described *Philopterus* (*Docophorus*) *reguli* based on an unknown amount of specimens from at least two collection events. At least one specimen was collected by another person, L. Jenyns, but the collection localities or methods of Jenyns' specimen and Denny's other specimens were omitted from the original description. Denny stated that the species showed "great variation" in the "colour and extent of the abdominal fasciae" [= tergal plates]. The host of this species was given as "Golden-crested Regulus (*Regulus aurocapillus*)" [= *R. regulus*]. At least some of Denny's specimens of this species were obtained by the British Museum [= Natural History Museum, London; hereafter NHML] (Gray 1852). Other specimens may or may not have been lost (cf. Thompson 1937; Clay 1947; Hopkins & Clay 1952; Mey 2020; see below).

Najer et al. (2020) reported that only a single specimen of *Ph. reguli* from Denny's collection remained at the NHML. They referred to this specimen as the "holotype", which is erroneous, as Denny did not designate any holotype. This specimen is here referred to as the "London syntype", for simplicity (see below). Subsequent reports of this species are few (see Najer et al. 2020 and below), and the only attempts at redescribing or illustrating the species prior to 2020 were published by Złotorzycka (1964b, 1977) and Złotorzycka & Lucińska (1976), as well as possibly by Fedorenko (1987; not seen). Notably, these redescriptions were done without reference to the London syntype, evidently based on the assumption that any *Philopterus* specimen found on *R. regulus* must be *Ph. reguli*.

There can be no argument about that both the illustrations and descriptions of *Ph. reguli* by Denny (1842), Złotorzycka (1964b, 1977), and Złotorzycka & Lucińska (1976) are subpar, and largely useless for identifying the species. The first useful illustrations of a species of *Philopterus* from this host are thus those published by Najer et al. (2020) and Mey (2020); there is no doubt that the species described and illustrated in these two publications represent the same species. Nor is it disputed that the species illustrated by Najer et al. (2020) and Mey (2020) is the one whose natural host is *R. regulus*. This louse species was reported by Najer et al. (2020) from numerous subspecies of *R. regulus* from across much of its range, as well as from *Regulus ignicapilla* (Temminck, 1820), and is here referred to as the "Brno species" for brevity, as the specimens illustrated by Najer et al. (2020) are deposited at the Moravian Museum in Brno, Czech Republic.

Najer et al. (2020) reported that the Brno species is not conspecific with the London syntype, with differences "e.g., in shape of head, shape of dorsal preantennal head plate [= dorsal anterior plate], thoracic and abdominal chaetotaxy, shape of subgenital plate". The London syntype was neither illustrated, nor photographed, nor described in text by Najer et al. (2020), and no detailed comparison between the London syntype and the Brno species was published, for which they were rightly criticized by Mey (2020). The London syntype is a female, meaning that details of the male genitalia that are believed to be crucial to species identity in *Philopterus* (see Gustafsson et al. 2022) cannot be examined. The statement that the London syntype specimen is not conspecific with the Brno species was not disputed by Mey (2020).

There is also no dispute that the redescription of Złotorzycka (1964b, 1977) and Złotorzycka & Lucińska (1976) are not based on specimens conspecific with the London syntype, but with the Brno species. Najer et al. (2020) examined at least part of the specimens examined by Złotorzycka to confirm this. They also examined some other specimens reported by other authors and found these to be conspecific with the Brno species. Thus, the species illustrated and described by Złotorzycka (1964b, 1977), Złotorzycka & Lucińska (1976), Najer et al. (2020), and Mey (2020), and the specimens on which these descriptions are based, are all conspecific, and constitute the Brno species.

To date, no other specimens conspecific with the London syntype are known. Najer et al. (2020) stated that the London syntype is different from all other *Philopterus* material they examined from any host in Regulidae. Beyond *Regulus regulus* and *Regulus ignicapilla*, Najer et al. (2020) did not state which other regulid species, if any, they examined material from. They also did not state whether any systematic effort was made to go through the Denny collection at the NHML to find other specimens that may be conspecific with the London syntype, but this is in any case not necessary. Moreover, no other species of *Philopterus* Nitzsch, 1818, have been described from any other host in the family Regulidae (Price et al. 2003). The closest relatives of the Brno species appear to parasitize tits and chickadees (Paridae; Najer et al. 2020; Mey 2020).

Thus far, there is no disagreement between Najer et al. (2020) and Mey (2020). However, Najer et al. (2020) declared that the London syntype is a straggler (specimen accidentally associated with a host) and suggested that most published records of *Ph. reguli* may not be this species. Instead, they gave a new name to the Brno species, *Philopterus gustafssoni* Najer et al., 2020. Moreover, they incorrectly refer to *Ph. reguli* as an "invalid name"[1] (Najer et al. 2020). If accepted, this treatment would mean that the London syntype retains the name *Philopterus reguli* Denny, 1842, and retains the type host *R. regulus*, but has an unknown natural host. Moreover, this would mean that *Ph. gustafssoni* is the valid name for the Brno species, whose type host and natural host is *R. regulus*. This would also be the only species of *Philopterus* known to parasitize *R. regulus* on a regular basis.

In contrast, Mey (2020) rejected the taxonomic decisions of Najer et al. (2020). As will be discussed below, Mey (2020) argued that the London syntype "is of dubious type status and cannot be used taxonomically". Instead, he rejected the London syntype, and designated a neotype and four "neoparatypes" (not recognized by the Code) for *Ph. reguli* Denny, 1842, from collections deposited at the Martin Luther University Halle-Wittenberg, in Halle (Saale), Germany. This neotype is here referred to as the "Halle neotype", for simplicity. If accepted, this would mean that the Brno species retains the name *Philopterus reguli* Denny, 1842 through this transfer of name-bearing type status. *Philopterus reguli* would retain the type host *R. regulus* and gain the natural host *R. reguli*. *Philopterus gustafssoni* would become a subjective junior synonym of *Ph. reguli*. Simultaneously, the London syntype would become nameless and have no known natural host but retain the "ghost type host" *R. regulus*, as that is the host upon which the specimen purportedly was found.

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[1] Confusingly, Najer et al. (2020) do not appear to mean that the name *Ph. reguli* is invalid in the sense of the Code, but invalid in the sense of "incorrect". No argument that the name is invalid in the sense of the Code was presented by Najer et al. (2020).

Due to the fundamental differences between these two taxonomic conclusions, overviews of the known history and identity of the London syntype and the name *Philopterus reguli* are necessary.

THE KNOWN HISTORY OF THE LONDON SYNTYPE

The history of Denny's collection following the publication of his monograph is only partially known. Already in 1838, he advertised for specimens from around Great Britain (Denny 1838), and many of the species he described in his monograph are based on specimens received by various correspondents. In some cases, he appears to have sent specimens back to their original collector. For instance, under *Nirmus stramineus*. Denny (1842: 139) stated that he was allowed "to retain [L. Jenyns' collection of lice] during the entire process of this work [i.e., the monograph]". The L. Jenyns in question is Leonard Jenyns, who later donated most or all of his collection of biological specimens to the Museum of Zoology in Cambridge, UK (Suarez Ferreira 2021). I have been unable to establish whether any Phthiraptera were included in this donation, which would be especially relevant, given that the "first specimen" of *Ph. reguli* was sent to Denny by L. Jenyns.

Part of Denny's collection was obtained by the NHML before 1852, when Gray (1852) listed all the specimens in the museum's possession. Gray stated that the museum "possesses the type specimens described and figured by [Henry Denny]" without qualification, implying that any and all specimens Denny considered types were obtained by the NHML. However, not all species described by Denny are noted as being in the NHML's possession, meaning that some types may have been deposited elsewhere. In Table 1, the species of *"Philopterus"* described by Denny are listed, along with information on which of these species were said to be in the NHML's possession by Gray (1852). Note that many of the species listed in Table 1 have since been moved to other genera or are considered synonyms of other species. Notably, types of *Ph. reguli* are listed as being in the possession of the NHML by Gray (1852). However, it should be noted that Article 72.4.7 of the Code states that a subsequent work stating that a specimen is a "type" does not necessarily mean this specimen is fixed as a type specimen in that work.

Denny's specimens were mounted on cards when they arrived at the NHML (Thompson 1937), but at some point between 1852 and 1937, at least part of the collection was cleared in KOH and slide-mounted by an unknown person. Thompson (1937) suggested that either Bruce F. Cummings or James Waterston may have been responsible for the slide-mounting but could not determine who. Cummings died in 1919, Waterston in 1930, suggesting that the transfer of specimens from cards to slides were done between 1852 and 1930.

The Denny slides have a certain style to them, not shared by most other slides at the NHML. Whoever mounted these slides used slide labels with a red outline for types, sealed the mounts with black rubber circles, and positioned the lice "horizontally" on the slide; the labels are also written in a neat cursive hand. This style of mounting, and the handwriting, are the same as that of type slides of species described by Cummings in the same collection. In contrast, the handwriting and overall mounting style of slides in the Waterston collection differs from this. Most likely, Denny's specimens were thus mounted by Cummings, or someone he employed to mount specimens for him. On the online photo database of slides at the NHML, all specimens from the Denny collection appear to be mounted in this way, indicating that they were all transferred from cards to slides by the same person(s) at the same time. Moreover, apart from Cummings type slides, no other slides in this collection appear to be mounted in the same style; however, no exhaustive search for other slides mounted in this style was conducted.

Thompson (1937) listed the specimens from the Denny collection present in the NHML at the time but did not note whether the specimens constituted types. Among the "*Philopterus*" species described by Denny (1842), Thompson (1937) listed specimens from only 24 species (Table 1); *Philopterus semisignatus* Denny, 1842, is not included in Thompson's list at all. Based on Thompson's list, specimens of nine species of "*Philopterus*" described by Denny (1842) are thus implied to have been lost between 1852–1937; as neither Denny (1842) nor Gray (1852) list any numbers of specimens, the loss may have been larger. A single female *Ph. reguli* is listed as being in the collection of the NHML by Thompson (1937).

However, Clay (1947) noted that Thompson (1937) had made several omissions, and that a total of 20 species not included in Thompson's list were actually present at the NHML. No details are given as to how these could have been overlooked, nor which these 20 species are (with two exceptions that are irrelevant to the present discussion). Hopkins & Clay (1952) marked all the species for which types were present in the NHML with an asterisk. Among the "*Philopterus*" species described by Denny (1842), this includes 32 species, omitting only two species that were noted as present by Gray (1852) (Table 1). Notably, *Ph. reguli* is noted by an asterisk. Again, as neither Gray (1852) or Hopkins & Clay (1952) include any information on the number of specimens from Denny's collection that were present, it is impossible to tell how many specimens may have been lost in the 100 years between these publications.

No further details are known about the London syntype until Najer et al. (2020) examined it. Under the current system at the NHML, the syntype has accession number

Table 1 (continued next page). History of the species of "*Philopterus*" described by Denny, listed in alphabetical order based on the name used by Denny (1842). Note that many of these species are today either moved to other genera or considered synonyms of other species (see Price et al. 2003). For each species, the number of collections or specimens mentioned, and the way they were mentioned, are summarized in the second column. Species are marked with "BM" in the third column if they are listed as being in the NHNL collection by Gray (1852); dashes ("–") indicate species not marked "BM" by Gray (1852). Species listed by Gray (1852) that were not described by Denny (1842) are not included. In the fourth column, we indicate the number of specimens of each species listed by Thompson (1937), with dashes where Thompson (1937) used dashes. For species that are absent in Thompson's list altogether, "NL" is given. Hopkins & Clay (1952) indicated with an asterisk species for which type material was present at the NHML, and these are here indicated with an asterisk as well. A more thorough, in-person examination of the collection at the NHML is needed to establish which specimens are still present there.

Species	Denny (1842)	Gray (1852)	Thompson (1937)	Hopkins & Clay (1952)
Philopterus alcedinis	single specimen, sent by L. Jenyns	–	–	–
Philopterus aquilinus	"tolerably common"; sent by W. Little, W. Jardine, Mr Calvert, G.R. Denny, Mr Thompson, as well as at least one collection by Denny himself	BM	–	*
Philopterus canuti	one specimen, sent by W.M. Tweedy	–	–	–
Philopterus ceblebrachys	specimens sent by A. Clapham, Mr Selby, and Mr Thompson	BM	3 ♀♀	*
Philopterus cephalus	Denny found it on two host species, and were sent specimens from at least five other collection events	BM	–	*
Philopterus chrysophthalmi	single specimen sent by Mr P.J. Selby	BM	–	*
Philopterus cincli	unknown number of specimens sent by A. Clapham, and Denny also collected	BM	–	*
Philopterus colymbinus	many specimens, sent by Mr Selby, Mr Tweedy, Mr Heysham, and collected by Denny himself. Additional specimens, considered a variety, from other host species, were sent by Mr Heysham and Denny's brother	BM	4 ♀♀	*
Philopterus conicus	single specimen collected by Denny	–	–	–
Philopterus cygni	multiple specimens from Mr Thompson, and from T.C. Heysham from two different host species	BM	4 ♂♂, 1 ♀	*
Philopterus fringillae	"communicated by Mr A. Clapham", no specimens mentioned	BM	2 ♀♀	*
Philopterus fusiformis	single specimen sent by Mr Thompson	–	–	–
Philopterus guttatus	unknown number sent from L. Jenyns, Denny subsequently found a single specimen	BM	3 ♂♂, 2 ♀♀	*
Philopterus humeralis	unknown number of specimens sent by Mr Thompson, and collected by Denny from three different host species	BM	4 ♀♀	*
Philopterus incompletus	unknown number of specimens collected by Denny himself	BM	2 ♀♀	*
Philopterus latifrons	Denny found it common on the host (implying he collected specimens from multiple birds?), and also received it from Mr Tweedy and Mr Doubleday, who sent him specimens from two hosts	BM	–	*
Philopterus limosae	unknown number of specimens sent by W. Thompson and G.R. Denny, from different host species	BM	1 ♀	*
Philopterus megacephalus	Denny found a single specimen	BM	–	–
Philopterus merguli	one specimen, sent by T.C. Heysham	–	–	–
Philopterus meropis	single specimen sent by W. Thompson	BM	2 ♀♀	*
Philopterus merulae	unknown number of specimens sent by W. Jardine, Mr Selby, and L. Jenyns who found it on two host species; Denny also collected a single specimen	BM	1 ♂, 7 ♀♀	*
Philopterus modularis	Multiple specimens sent by Denny's brother	BM	2 ♀♀	*
Philopterus nisi	unknown number of specimens sent by L. Jenyns and G.R. Denny	BM	1 ♂, 3 ♀♀	*
Philopterus ostralegi	"common upon the Oyster-catcher" = multiple collections?	BM	2 ♂♂, 1 ♀	*
Philopterus pallescens	unknown number of specimens sent by L. Jenyns and G.R. Denny	BM	–	–

Table 1 (continued).

Species	**Denny (1842)**	**Gray (1852)**	**Thompson (1937)**	**Hopkins & Clay (1952)**
Philopterus pari	unknown number of specimens sent by L. Jenyns, and Denny found specimens on two host species	BM	1 ♂	*
Philopterus passerinus	unknown number of specimens sent by L. Jenyns and G.R. Denny, Denny also collected a single specimen	BM	1 ♀	*
Philopterus pastoris	multiple specimens, sent by W. Thompson	BM	1 ♀	*
Philopterus picae	one specimen, from L. Jenyns	BM	1 ♀	*
Philopterus plataleae	"I found an abundance of this insect" on a single host	BM	1 ♂, 5 ♀♀	*
Philopterus platygaster	collected by Denny himself, with additional specimens from two hosts sent by his brother	BM	–	*
Philopterus ralli	unknown number of specimens sent by L. Jenyns	–	–	–
Philopterus reguli	one specimen form L. Jenyns, and Denny subsequently collected more	BM	1 ♀	*
Philopterus rubeculae	unknown number of specimens collected by Denny, and additional specimens sent by L. Jenyns from two host species	BM	1 ♂, 3 ♀♀	*
Philopterus semisignatus	unknown number of specimens sent by W. Thompson	BM	NL	*
Philopterus testudinarius	unknown number of specimens sent by Mr Thompson and Mr Heysham	BM	–	*
Philopterus thalassidromae	unknown number of specimens sent by W.M. Tweedy	BM	2 ♀♀	*
Philopterus turdi	"specimens" indicate multiple, collected by Denny himself	BM	2 ♀♀	*
Philopterus upupae	unknown number of specimens sent by W.M. Tweedy and T.C. Heysham	BM	5 ♂♂, 2 ♀♀	*
Philopterus variabilis	unknown number of specimens sent by W.M. Tweedy	BM	1 ♀	*

NHMUK010710741, and is located in the Denny collection. According to Najer et al. (2020), all other specimens labelled as *Philopterus reguli* at the NHML represent other genera from outside the *Philopterus*-complex; these specimens are not in the Denny collection and are mounted in different style.

Thus, at least one type specimen of *Ph. reguli* was listed by Gray (1852), exactly one was listed by Thompson (1937), at least one was listed by Hopkins & Clay (1952), and exactly one was found in that collection by Najer et al. (2020). If there were ever more than one type specimen of *Ph. reguli* in the NHML's possession, those specimens must have been lost before 1937, after which the number of type specimens of *Ph. reguli* in this museum appears to be constant. If specimens disappeared from the collection, it is most likely that this happened before or during the slide-mounting; if it is assumed that Cummings mounted these specimens, the time window for their loss must be between 1842–1919. This is too long a period with too much change at the NHML to establish any more detail. However, no evidence for such a loss has ever been presented, and there is no published evidence to suggest we should not take the identity of the London syntype at face value. Any contrasting opinion would need a sounder basis of argument than has hitherto been presented.

HOW MANY "SYNTYPES" DID DENNY HAVE?

Najer et al. (2020) erroneously referred to the London syntype as the "holotype", overlooking the fact that only the original author can designate a holotype, and that subsequent authors can only designate lectotypes (from a syntype series) or neotypes. It is clear from reading his monograph that Denny (1842) examined multiple specimens before publication: he stated that he first examined a single ["first"] specimen, and that he "since then have obtained others". Mey (2020: 160) pointed out the error of Najer et al. (2020) and correctly stated that "several individuals ("syntypes") were available [to Denny]". Mey (2020) at several points refer to the London syntype as the "remaining" or "surviving" syntype.

Article 72.4.1 of the Code states that the "type series of a nominal species-group taxon consists of *all the specimens included by the author* in the new nominal taxon [...] except any that the author expressly excludes from the type series [...] or refers to as distinct variants (e.g. by name, letter or number), or doubtfully attributes to the taxon" (my italics). Based on this Article, it is clear that at the time of printing of Denny's monograph, more than one syntype existed, as no express exclusion of any specimens from the type series was made by Denny. Denny's text implies a minimum of three syntype specimens. Assuming that the London syntype was included among these syntypes, it is fair to say that at present only a single syntype of *Ph. reguli* is known to exist.

As a side note, the above is based on our modern concept of a syntype and may not be consistent with how Denny or people at his time saw it. The absence of more than one specimen of *Ph. reguli* at the NHML may be due to Denny only considering his first specimen a type, and the others non-types, similar to how for instance Najer et al. (2020) listed only a small number of specimens under "Holotype" and "Paratype" for the Brno species and left the vast majority as "Other material". The cases of *Nirmus* [= *Quadraceps*] *alcae* Denny, 1842, and *Nirmus* [= *Brueelia*] *stramineus* Denny, 1842, almost exactly parallel that of *Ph. reguli*. Denny first saw a single specimen and then obtained others, these are listed by Gray (1852), and only a single specimen of each is today present in the NHML, mounted in the same style as *Ph. reguli*. However, whereas Thompson (1937) lists only a single *Nirmus alcae*, he lists a total of three *Nirmus stramineus*, suggesting that there is no uniform pattern.

While the above scenario is a possibility, it can be overruled by Article 72.4.1 of the Code, which unequivocally shows that Mey (2020) is correct in his statement that more than one syntype existed at some point, whether or not they were considered as such by Denny.

IS THE LONDON SYNTYPE A SYNTYPE?

Mey (2020) asserted that "it can be shown that no name-bearing type of *Philopterus reguli* ex *Regulus regulus* any longer exists […] and the only existing "syntype" is of dubious origin". It is unclear what this is based on.

No evidence has been presented by either Najer et al. (2020), Mey (2020) or anyone else to suggest that the London syntype is not a (syn)type of *Ph. reguli*, as stated on the slide label. It is clear that syntypes were present at the time of the publication of Denny's monograph in 1842, that types described and figured in this monograph were in the possession of the NHML in 1852, that at least one specimen of *Ph. reguli* from the Denny collection was present at the NHML in 1937, and again in 1952. There is no evidence presented that any specimens of *Ph. reguli* have been lost from the NHML after 1952, nor that the specimen reported in 1952 is not among those reported in 1842, 1852, or 1937. The London syntype may not be one of Denny's original syntypes, but that has to be demonstrated rather than asserted.

Above all, if the London syntype had been conspecific with the Brno species, there would have been no question that the London syntype was a valid syntype. This is thrown in doubt only because two species are involved here, and the London syntype does not correspond to the Brno species. I find it impossible to rule out, based on our current knowledge, that the London syntype is a genuine syntype that has been handed down to us from Denny, a journey that is documented by at least four publications now (Gray 1852; Thompson 1927; Hopkins & Clay 1952; Najer et al. 2020).

I therefore find that the neotype designation of Mey (2020) is in violation of Article 75.1 and 75.3.4 of the Code, as it cannot be assumed, and has not been demonstrated, that no name-bearing types exist. Furthermore, I find the neotype designation to be in violation of Article 75.3.4 as Mey (2020) does not outline any "steps that had been taken to trace" any other syntypes, for instance those potentially sent back to L. Jenyns (see above). As the London syntype was never lost, Article 75.8 does not come into effect; however, if additional specimens are found, for instance at the Museum of Zoology, Cambridge, this Article may also become relevant.

CAN THE LONDON SYNTYPE BE IDENTIFIED?

As neither Najer et al. (2020) nor Mey (2020) included any text description, photo, or illustration of the London syntype, these publications cannot be used to ascertain whether this specimen can be identified today. However, the photo of the London syntype provided by the NHML homepage does not appear to be destroyed, distorted, or otherwise impossible to identify, given adequate study and comparison with other specimens. *Philopterus* specimens are relatively common in museums across the world; the NHML alone hosts over 3000 slides with *Philopterus*, many of which contain more than one specimen. Most of this material is undescribed, and many of the described species are presently unidentifiable.

Systematically comparing the London syntype with all other species of *Philopterus* at the NHML and other collections would be time-consuming, but there is no published evidence that suggest it would be impossible. Moreover, not all slides would need to be compared. For instance, as Najer et al. (2020) stated that the London syntype does not have the row of pronotal setae found in the Brno species, all species bearing these setae can be excluded from the comparisons. It is also evident from the digital photo of the London syntype that it is probably morphologically different from the group of *Philopterus* that is normally found on crows and allies (Corvidae; Price & Hellenthal 1998) and the group that parasitizes swallows (Hirundinidae; Gustafsson et al. 2022). As more species of *Philopterus* are described and redescribed, and the morphological variation within this genus becomes better known, other groups of *Philopterus* may also be possible to exclude from comparisons. Moreover, all *Philopterus* species that do not plausibly occur in the UKs or Europe may be excluded. No type locality of *Ph. reguli* was given by Denny (1842), but as his aim was to treat the species found in the UK, the specimens of *Ph. reguli* he examined are likely from this region, even if the host association is incorrect. That would limit the number of taxonomically relevant comparisons to a few dozen. This may have its own taxonomical consequences, especially if the London syntype is found to be conspecific with another described species.

It is worth pointing out that a substantial amount of the European species of *Philopterus* are formally described but largely unidentifiable without comparison with type specimens. This is due to the unfortunate tradition in European louse taxonomy to consider Fahrenholz's rule to be strictly applied to louse evolution, and thus every host species having its own louse species (Gustafsson & Najer 2022). This applies not least to the many species described by Jadwiga Złotorzycka, which are often only known from a short, uninformative text, some measurements, and outline drawings of some morphological characters, with no or little detail. The difficulties in identifying the London syntype may thus be more due to the poor taxonomic practices of, for example, Złotorzycka, than with the state of the London syntype itself.

In my opinion, it has not been shown that the London syntype is unidentifiable. If it is accepted that this specimen is a syntype, as I provisionally do here, this would mean that the neotype designation of Mey (2020) is in violation of Article 75.5 of the Code, which allows for neotype designation only when the name-bearing type is judged to be unidentifiable. This has, in my opinion, not been shown either by Najer et al. (2020) or Mey (2020), although a reexamination of the London syntype may very well show that this is correct.

CAN "THE FIGURE 4 SPECIMEN" BE IDENTIFIED TODAY?

Quite separate from the possibility of identification of the London syntype is the identification of the specimen illustrated in Denny (1842; plate VI, fig. 4; hereafter: "the Figure 4 specimen"). This is particularly important since Article 75.3.5 states that in order to be validly designated, a neotype must be shown to be "consistent with what is known of the former name-bearing type from the original description and from other sources". If it is assumed that the London syntype is not a syntype, but a contamination, mix-up or other error, then the neotype needs to be consistent with what is known from the only other source of data we have, Denny's original description and illustration. Notably, "other sources" correspond only to sources about the original name-bearing types, not about the species as such, or the prevailing understanding of the species.

An analysis of the Figure 4 specimen is necessary, because if it is found that the neotype designation of Mey (2020) is invalid, and it is accepted that the London syntype either is not a genuine syntype or does not correspond to the taxon *Philopterus reguli* as presently understood, it is possible to select the specimen on which Figure 4 is based as the lectotype of *Ph. reguli*, following Article 74.4. This Article also explicitly states that "the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation". This means that it is possible to stabilize the nomenclature of *Ph. reguli* by reference to the only specimen that can unequivocally be stated to have represented this species at the time of the publication of Denny's monograph.

As stated above, Denny's original description and illustration are insufficient to identify *Philopterus reguli*. It could be argued that nothing in the description can be used to definitely identify this species even to the genus level, as louse genera are understood today. Similarly, Denny's original drawing could be virtually any species of *Philopterus*; more than that, it could show virtually any species in the *Philopterus*-complex and is not clearly different from representatives of some other genera that are more distantly related. Two characters are particularly noteworthy.

THE PRONOTAL SETAE

As noted above, the Brno species and the Halle neotype both have a row of setae on the posterior margin of the pronotum, called the *pronotal submarginal setae* or *psms sensu* Mey (1994). These setae are indicative of a small group of species within *Philopterus*, which Złotorzycka & Lucińska (1976: 286) termed the "*reguli* species group". The limits of this group have varied (Złotorzycka & Lucińska 1976; Mey 1983, 1988, 2020; Najer et al. 2020), but both Najer et al. (2020) and Mey (2020) agreed that the Brno species should belong to this group.

The chaetotaxy of *Philopterus reguli* is ignored almost completely in Denny's description, and only the setae of the pterothorax (as "metathorax") are mentioned: "posterior margin ciliated with stiff hairs" (Denny 1842: 91). In Figure 4, the pteronotal setae are illustrated, but the pronotal setae are not. The pronotal and pteronotal setae appear to be of roughly the same length and thickness in both the illustrations of Najer et al. (2020) and Mey (2020). While single, more lateral setae may have been overlooked by Denny, it seems likely that he would have been able to observe rows of setae on both segments and illustrated both sets. At the very least, no argument against this hypothesis has been published.

However, the lack of pronotal setae in the Figure 4 specimen should not automatically be interpreted as a difference between this specimen and the Brno species. Pronotal setae appear to be absent in all species illustrated by Denny. Notably, this includes not only species in which the pronotal setae are even longer and stouter than those of *Ph. reguli*, such as "*Goniocotes hologaster*" (Nitzsch, 1818) [= *Goniocotes gallinae* (De Geer, 1778)] (Denny 1842: plate XIII, fig. 4), but even another species placed in the *reguli* species-group, *Philopterus pallecens* Denny, 1842 (ibid., plate I, fig. 8). It would appear that for whatever reason Denny did not see any pronotal setae on any of his specimens. Possibly, this was due to the mounting method that may have damaged pronotal setae, or the rudimentary microscopy technology of the time. The real reason will never be known.

Thus, presence or absence of pronotal submarginal setae in the illustration of the Figure 4 specimen may not be significant for establishing its identity, nor to establish the identity of *Philopterus reguli*. However, the apparent lack of these setae in Denny's illustration remains a character that any neotype would need to consistent with in order to be validly designated.

THE TRABECULA OR CONI

All members of the *Philopterus*-complex have trabeculae, which are almost always longer than the antennal scape (e.g., Mey 2004; Gustafsson et al. 2022). This is a defining character of the complex, as trabeculae are not known from any other group of lice. In the Brno species, Najer et al. (2020) illustrated the trabeculae as almost reaching the distal end of the pedicel (ibid., fig. 6c), whereas Mey (2020) illustrated them as reaching around half the length of the pedicel in his "neoparatypes" (ibid., fig. 6). In both illustrations, these structures are clearly illustrated as trabeculae, rather than coni (sensu Clay 1946). Although there are developmental and structural differences between these two structures, the most pertinent aspect for the present discussion is that coni are almost invariably simply triangular, whereas trabeculae have a narrowed proximal base, a swollen mid-section, and a tapering distal end. Especially in older illustrations, where the term "trabecula" is used for both structures, the overall shape may be helpful to determine what structure is actually illustrated.

This difference in shape is visible in some, but not all, of Denny's other illustrations. For instance, trabeculae are illustrated in their characteristic shape for species such as *Philopterus picae* Denny, 1842 (plate I, fig. 9) and *Philopterus communis* Denny, 1842 (plate 5, fig. 10). In illustrations of species today placed in *Philopterus*, the trabeculae seem to invariably be drawn as much longer than the scape, regardless of whether the narrowed proximal section is illustrated. In contrast, species belonging to other groups in which trabeculae are not found have either long or short structures drawn; for instance, *Philopterus* [= *Penenirmus*] *pari* Denny, 1842 (plate VI, fig. 6a). This reflects the fact that in some groups the coni will be as long as the trabeculae of the *Philopterus*-complex but shaped differently and of a different developmental origin. In short, the generic identity of Denny's illustrated specimens cannot be assumed based on the trabeculae or coni when these are longer than the scape, unless they have the characteristic shape of trabeculae, but if they are at most as long as the scape, they are likely coni rather than trabeculae.

This is notable as in the detailed drawing of the antenna of the Figure 4 specimen (Denny 1842; plate VI, fig. 4a), the trabecula is entirely absent. This is not the case with any other *Philopterus* species illustrated by Denny; the illustration of *Ph. pallescens* Denny, 1842 (plate I, fig. 8a) appears to be an exception, but the illustrated specimen seems to be a nymph, and trabeculae may be significantly smaller in nymphs than in adults in *Philopterus* (Mey 1994). However, coni are not illustrated for in several illustrations of species that are not in the *Philopterus*-complex. Moreover, no trabeculae are visible in the full-body illustration of the Figure 4 specimen either (*ibid.,* plate VI, fig. 4), whereas these are clearly illustrated in all other species of *Philopterus*. In the text description, Denny (1842) stated that the trabeculae of *Ph. reguli* are "small".

The obvious conclusion to this observation is that the Figure 4 specimen is also not conspecific, or even congeneric, with the Brno species or the Halle neotype. Moreover, as Najer et al. (2020) examined the London syntype and considered it to belong to *Philopterus*, it must also have trabeculae, and thus not be congeneric with the illustrated specimen. The trabeculae are visible in the photo of the London syntype provided by the NHML homepage.

THE IDENTITY OF FIGURE 4

The variation of two morphological characters across the specimens and species discussed here is summarized in Table 2. Based on this data, it appears that the identity of the Figure 4 specimen is at least consistent with the text description, but is not consistent with either the London syntype, the Brno species, or the Halle neotype. Potentially, as many as three species are involved: a species with small trabeculae (= coni?) and possibly no *psms* (Figure 4 specimen and also the text description), a species with large trabeculae and no *psms* (London syntype), and a species with large trabeculae and *psms* (Brno species and Halle neotype). At the very least, it cannot be excluded that the Figure 4 specimen represents a different species than the Brno species, regardless of the status of the London syntype.

If the above arguments are correct, the (presumably now lost) Figure 4 specimen is also not conspecific with *Philopterus reguli* as we currently understand the taxon, and should not be designated a lectotype, if current prevailing usage is to be maintained. That would mean that if prevailing usage of *Ph. reguli* is to be maintained, a neotype is needed, as neither of the two syntypes that we have any information about are conspecific with the Brno species.

Table 2. Summary of the morphological characters relevant for identifying the various specimens discussed here, and their distribution across various illustrations and descriptions. Data for the London syntype is taken from Najer et al. (2020) and the photo of the specimen on the NHML homepage.

character	original description (Denny 1842)	Figure 4 specimen (Denny, 1842)	London syntype	Brno species (Najer et al. 2020)	Halle neotype (Mey 2020)
Pronotal submarginal setae	not mentioned	not illustrated, may be absent	absent	present	present
Trabeculae	"small"	not illustrated	large	large	large

This close analysis of the Figure 4 specimen implies that regardless of the status of the London syntype, Denny's original type series appears to have included at least one straggler, which unfortunately appears to be the one specimen he illustrated in Plate VI, fig. 4. Possibly, the Figure 4 specimen is the one Denny obtained first, from L. Jenyns, but this is presently impossible to establish, unless the Jenyns collection of lice is still extant and includes this specimen.

It is difficult to establish from Denny's illustration what the Figure 4 specimen may have been, if it is not conspecific with the Brno species. Overall, it appears smaller and slenderer than most other *Philopterus* species illustrated by Denny, and more slender than *Ph. gustafssoni* as illustrated by Najer et al. (2020). However, as the specimen is drawn from a card-mounted specimen rather than a slide-mounted specimen, these differences may be illusory. Other aspects of the illustration, such as the apparently medianly divided tergopleurite IX+X, may be erroneous; this tergopleurite is medianly continuous in all *Philopterus*-complex genera (e.g., Mey 2004; Najer et al. 2020; Gustafsson et al. 2022). In general, there are so many aberrant aspects of this illustration that any genus-level identification will require intentionally ignoring some clearly illustrated characters while accepting others. It is therefore best to consider the Figure 4 specimen unidentifiable to genus level, and possibly either fanciful or chimeric or based on an aberrant individual.

CONSERVATION OF PREVAILING USAGE

Mey (2020) does not argue for the need for a neotype, and the synonymization of *Ph. gustafssoni* with *Ph. reguli*, out of idleness or spite. Instead, his actions go to the heart of what the International Rules of Zoological Nomenclature are about: stability and predictability of usage of names for animals. Article 75.6 of the Code allows a researcher to request that the Commission set aside any name-bearing type if it is found not to be "in taxonomic accord with the prevailing usage of names and stability and universality is threatened thereby." Mey (2020: 160) explicitly established his neotypes "in the interest of the stability of this taxon" and mentioned that the Commission may "have to be called upon to take a definitive decision if the proposal meets with any well-founded resistance". It is difficult to disagree with Mey that the species normally found on *Regulus regulus* should have the name that has been assigned to it throughout the last 180 years, even if by capricious fate the specimens to which this name was originally attached are now known to represent a different species, which may not be identifiable. Regardless of anything else, Mey's goal here is laudable, and should perhaps be emulated more widely to secure nomenclatural stability among poorly identifiable species of lice.

The case for stability would be that the *Philopterus* species naturally occurring on *R. regulus* in Europe has been assumed to be *Ph. reguli* since Denny (1842) first described the species. Both Najer et al. (2020) and Mey (2020) listed some instances where this name has been applied to the species of *Philopterus* living on *R. regulus* and *R. ignicapilla*, but a casual search revealed many more; these are listed in Table 3, but this list may also not be exhaustive. In total, at least 30 publications over the last 180 years have used the name *Ph. reguli* for the species of *Philopterus* that occurs naturally on *R. regulus* and *R. ignicapilla*. In contrast, the name *Ph. gustafssoni* has so far only been used by members of the same research team as Najer et al. (2020) (Table 3).

If a request was put to the Commission to set aside any name-bearing types of *Ph. reguli* and recognize a neotype, this list of usages may be used to establish prevailing usage in favour of the petition. In general, more published usages of a name would suggest that stability of nomenclature would be disrupted if action is not taken to designate a neotype. However, it should be noted that the Commission does not operate on a principle of precedence, and each case is judged on its own merits. There is therefore no "magic number' of usages that are needed to establish prevailing usage. Moreover, it is ultimately up to the louse research community which name will be used, as the Commission has no enforcing capabilities if researchers are dissatisfied with their ruling.

COLLECTION HISTORY OF *PH. REGULI*

The first publications that report specimens of *Ph. reguli* other than the Denny specimens were Balát (1958) and

Table 3 (continued next page). Summary of published uses of the name *Docophorus/Philopterus/Docophorulus reguli* (Denny, 1842) or *Philopterus gustafssoni* Najer et al. (2020) based on references provided by Najer et al. (2020) and Mey (2020), as well as some sources omitted by these authors; list is not necessarily complete. Two sources listed by Najer et al. (2020) were not seen: 1) Kravtsova (1998) is an unpublished PhD thesis; 2) Fedorenko (1987) is a volume in a series on the fauna of Ukraine. Judging from other entries in Fedorenko (1987), there may be illustrations and a description of *Ph. reguli* in this publication similar to that of Złotorzycka (1977). These two publications are not listed below. Records of "*Philopterus subflavescens*" listed by Najer et al. (2020) are also not listed, as these records have no influence on the present case. For each publication, the following data is listed: 1) Information provided (i.e., what data about the lice of *Regulus regulus* is given?); 2) Data used (i.e., does this publication rely on examined specimens or is it a list of previous literature record etc.?); 3) Method of identification (i.e., were published sources or comparisons with type specimens used to establish identity of the lice? Note that only sources explicitly referring to the identity of *Ph. reguli/gustafssoni* are listed here, even if other sources were used to identify other species mentioned. If no method is explicitly given for *Ph. reguli/gustafssoni*, but Material and Methods include references that include descriptions of *Ph. reguli/gustafssoni*, these are listed here under the assumption that this is the method used); 4) Problem with changing name? (i.e., would changing the name from *Ph. reguli* to *Ph. gustafssoni* have effects beyond just the name change, e.g., by disconnecting published data other than locality records from the published name?). If the only change necessitated by the taxonomic acts of Najer et al. (2020) is a change of name in a regional, national or taxonomic checklist, this is not here considered a problem. A problem, as defined here, only appears if a publication contains any amount of secondary data (e.g., descriptions, measurements, host associations, prevalence data, etc.). This includes e.g., morphological data, ecological data, or life-history data.

Source	Region	Information provided	Data used	Method of identification	Problem with changing name?
Philopterus reguli					
Denny (1842)	UK	original description and illustration	specimens	original description	yes
Gervais (1844)	–	listed in global list of lice	description	Denny (1842)	no
Gray (1852)	UK	Included in list of specimens obtained	–	Denny (1842)	no
Giebel (1874)	–	included in a list of species the author did not examine	–	Denny (1842)	no
Piaget (1880)	–	listed in global list of lice	–	Denny (1842)	no
Harrison (1916)	–	listed in global checklist of lice	literature record	–	no
Thompson (1937)	–	included in list of specimens	london syntype?	–	no
Séguy (1944)	France	listed in list of species presumably occurring in France	–	–	no
Hopkins & Clay (1952)	–	listed in global checklist of lice	london syntype?	specimen	no
Negru (1958)	Romania	national records; measurements; new host record	specimens	Denny (1842)?	yes
Balát (1958)	Bulgaria	national records	specimens	none stated	no
Ash (1960)	Sweden	national records; prevalence data	specimens	none stated	yes
Bechet (1961)	Romania	national records	specimens	none stated	no
Złotorzycka (1964b)	Poland	redescription and illustration	specimens	none stated	yes
Rékási (1973)	Hungary	national records	specimens	none stated	no
Eichler & Hackman (1973)	Finland	listed in national checklist	specimens	none stated, possibly Złotorzycka (1964b)	no
Złotorzycka & Lucińska (1976)	Poland	redescription and illustration	specimens	none stated	yes
Balát (1977)	Czechoslovakia	listed in national checklist	specimens	none stated	no
Złotorzycka (1977)	Poland	redescription and illustration	specimens	none stated	yes
Rékási (1993)	Hungary	listed in national checklist	literature record	none stated	No

Table 3 (continued).

Source	Region	Information provided	Data used	Method of identification	Problem with changing name?
Hackman (1994)	Finland	listed in national checklist	literature record	previous record accepted	No
Mey (2003)	Germany	listed in national checklist	literature record	none stated	No
Price et al. (2003)	–	listed in global checklist	literature record	–	No
Adam & Sandor (2004)	Romania	national records	specimens	presumably Złotorzycka (1977)	No
Palma & Jensen (2005)	Faroe Islands	listed in regional checklist	specimens	none stated	No
Martín Mateo (2006)	Spain	listed in national checklist	literature record?	none stated	No
Ilieva (2009)	Bulgaria	listed in national checklist	literature record	previous record accepted	No
Vas et al. (2012)	Hungary	listed in national checklist	literature record	previous record accepted	No
Dik et al. (2017)	Turkey	national records	specimens	Złotorzycka (1964b)	No
Rékási et al. (2018)	Romania	listed in regional checklist	literature record	previous record accepted	No
Malysheva & Tolstenkov (2018)	Russia	regional and national record	specimens	none explicitly stated, possibly Fedorenko (1987)	No
Gustafsson et al. (2019b)	Sweden	listed in national checklist	literature record	previous record accepted	No
Philopterus gustafssoni					
Najer et al. (2020)		redescription	specimens	specimens	Already changed
Najer et al. (2021)	Azores, Czechia	phylogenetic data	specimens	Najer et al. (2020)	Already changed
Mey (2020)		redescription	specimens	Specimens; Najer et al. (2020)	yes
Oslejskova et al. (2020)	Azores	regional records; prevlence data	specimens	Najer et al. (2020)	already changed
Oslejskova et al. (2021)	Slovakia	listed in national checklist	specimens	None stated; presumably Najer et al. (2020)	Already changed

Negru (1958). Balát (1958) collected nymphs and eggs from the type host of *Ph. reguli*, whereas Negru (1958) collected both adults and nymphs from at least two host birds, both of which were the non-type host *R. ignicapilla*. After that, Ash (1960) collected a small number of specimens from the type host in Sweden, and Bechet (1961) reported an unknown number of specimens from the type host from Romania. None of these authors included any description or illustration of their specimens, nor any indication as to how their specimens were identified.

For all these publications, the only available illustrations and descriptions were those of Denny (1842), and the only known specimens were those allegedly at the NHML (Hopkins & Clay 1952). As none of these authors indicated that they examined the London syntype or any other specimen at the NHML, and it is clear from Denny's illustration and description that his species is not conspecific with the species normally found on *R. regulus* and *R. ignicapilla*, it must be concluded that these early records were identified based on host associations and a mistaken conflation of type host and natural host. This is particularly obvious in the case of Balát (1958), as he only collected nymphs, and Denny (1842) only described and illustrated the adult.

Złotorzycka (1964b) made the first attempt to redescribe *Ph. reguli* based on specimens she had obtained in Poland. Złotorzycka (1977) and Złotorzycka & Lucińska

(1976) also redescribed *Ph. reguli*, and these descriptions can be treated together. In the 1964b description, only the dorsal anterior plate is illustrated (Złotorzycka 1964b: fig. 5i) and the text description is short and useless for identification even to genus level. Złotorzycka & Lucińska (1976) had access to more specimens, which resulted in a more thorough attempt to illustrate and describe the species, but the lack of detail still makes it largely impossible to identify other specimens definitely from this account. Nevertheless, the 1976 illustrations are largely congruent with the more detailed illustrations of Najer et al. (2020) and Mey (2020). The 1977 account largely reuses the same illustrations as the 1976 account, but adds illustrations of the trabecula, parts of the mouthparts, and some of the tergopleurites. The text, in the form of a dichotomous key, is more detailed than previous accounts. Both Najer et al. (2020) and Mey (2020) agreed that the species illustrated in these three publications, and the specimens Złotorzycka used for those illustrations, are conspecific with the Brno species. Najer et al. (2020) examined most of these specimens in person, and there seem to be no reason to doubt this judgement.

Fedorenko (1987) may also have illustrated and redescribed *Ph. reguli*, but I have not seen this publication, and cannot judge whether this publication is useful. Based on other drawings by Fedorenko, any potential redescription of *Ph. reguli* in this book may be similar to that of Złotorzycka (1977).

Starting in 1964, it is thus theoretically possible to identify a species identified as *Philopterus reguli* without reference to Denny's illustrations or description. However, it is clear that Złotorzycka did not examine the London syntype, nor examine the published description and illustration well. For instance, Złotorzycka (1977) illustrated a long, typically shaped trabecula for *Ph. reguli*, which (as discussed above) are explicitly stated to be small in this species by Denny (1842). These trabeculae are also visible in the head outlines published by Złotorzycka & Lucińska (1976) and Złotorzycka (1977). Złotorzycka's illustrations must thus be assumed to be based on specimens she had identified by host-association, not by morphology. Here, if not earlier, the idea that any *Philopterus* specimens found on *R. regulus* must be *Ph. reguli* creeps into the usage of this name, thus establishing the pattern of misidentification that eventually led to the disagreement between Najer et al. (2020) and Mey (2020).

Three other publications during the 1970s are based on collected specimens (Rékási 1973; Eichler & Hackman 1973; Balát 1977). Of these, Eichler & Hackman (1973) and Balát (1977) merely list species present in previous collections (P. Krüger's and K. Pfleger's, respectively) and provide no data on how many specimens are present, the age and sex distribution of these, and how they were identified. Eichler & Hackman (1973) mistakenly refer to the author of *Docophorulus* [= *Philopterus*] *reguli* as "Złotorzycka 1964[b]". Rékási (1973) stated that he found one adult and three nymphs on a single host, and that this was a new record for Hungary, but did not state how these specimens were identified.

Two subsequent uses of the name *Ph. reguli* from Hungary (Rékási 1993; Vas et al. 2012) are updates of Rékási's (1973) checklist, which also do not contain any data on how these specimens were identified and appear to mainly refer back to the original record by Rékási (1973). Similarly, the usages of Hackman (1994), Mey (2003), Ilieva (2009), Rékási et al. (2018), and Gustafsson et al. (2019) are merely inclusions in national checklists that accept previous literature records, and do not attempt to detail how these previous records were identified. The usage by Martín Mateo (2006) also appears to fall into this category. Palma & Jensen (2005) evidently studied novel specimens purportedly of *Ph. reguli*, but did not detail in their checklist how many specimens were examined, nor how specimens were identified.

The next records that include actual specimens purported to be *Ph. reguli* are Adam & Sandor (2004; Romania), Dik et al. (2017; Turkey), and Malysheva & Tolstenkov (2018; Kaliningrad exclave of Russia). None of these publications are explicit in how the specimens were identified, but all cite sources that include illustrations and descriptions of *Ph. reguli sensu* Złotorzycka (1964b). It may thus be safe to assume that the specimens reported in these publications, as well as those by, for example, Palma & Jensen (2005) and Martín Mateo (2006), also represent the Brno species; however, this needs to be verified.

DATA PROVIDED

It is clear from this brief overview of the published record of *Philopterus reguli* that almost all data provided are just new locality (or national) records. *Philopterus reguli* is listed in national checklists for Bulgaria, "Czechoslovakia", Finland, Hungary, Romania, and Sweden, and for regional checklists of the Danube delta, the Faroe Islands, and the Community of Madrid (references in Table 3). In some of these cases, no detailed collection data was provided in the checklists or their sources, and inclusion of *Ph. reguli* in national or regional checklists is thus sometimes asserted rather than demonstrated. Almost invariably, no specific specimen slides, with deposition data, are included in the checklists or their primary sources.

Apart from geographical distribution, the only additional data given by the authors listed in Table 3 is the following: Negru (1958) added some measurements, noted a co-occurrence of *Ph. reguli* and *Ricinus frenatus* (Burmeister, 1838) on the same host, and added *R. ignicapilla* as a host species; Ash (1960) added some prevalence data; Złotorzycka (1964b, 1977), Złotorzycka & Lucińska (1976) and possibly Fedorenko (1987) added illustrations and redescriptions, but these are not of the same species as *Ph. reguli* as described by Denny (1842). Beyond that, 180 years of research has not added anything to our knowledge of *Philopterus reguli*, and most of the data we have applies to a different species than *Ph. reguli sensu* Denny (1842).

In contrast, under the name "*Philopterus gustafssoni*", the Brno species has been provided with a complete description (Najer et al. 2020), many illustrations and photos (Najer et al. 2020; Mey 2020), new regional records (Oslejskova et al. 2020, 2021), genetic data (Najer et al. 2020, 2021), prevalence data (Oslejskova et al. 2020), and new host associations (Najer et al. 2020). It is fair to say that the majority of the data we have on the Brno species, whatever it is named, has either been published under the name *Ph. gustafssoni*, or could easily be redirected to this name without problem.

The question becomes: what is the disruption of stability if Denny's species is considered a *nomen dubium* that cannot be identified until any other potential extant syntype specimens are rediscovered, and the name *Ph. gustafssoni* is used for the Brno species? This question has no clear answer. However, there is no secondary literature on the Brno species (e.g., ecology, life-history, phylogenetics, behaviour) that would be easily overlooked by non-taxonomists if there was a change in name. The species is not used as a model organism, and it appears to be comparatively rare, given the few specimen-based records that have been published. Finally, both Balát (1977) and Oslejskova et al. (2021) published checklists of the "Czechoslovakian" louse fauna. Both checklists include the Brno species, but different names are used for it. This suggests that for most of the known uses of *Ph. reguli*, there will be no problem substituting one name for the other.

PUTTING THE CART BEFORE THE HORSE

It is clear that the present conundrum is the direct result of a conflating of the concepts of type host and natural host, and an overreliance on extrinsic characters such as host associations rather than intrinsic characters such as morphology. Any of the many researchers who have either worked at the NHML, visited this museum, borrowed specimens from this museum, or who has otherwise worked with *Philopterus* could at any time have noticed that neither the London syntype nor the Figure 4 specimen is conspecific with the species of *Philopterus* normally found on *R. regulus*. Instead, the assumption of host specificity and taxonomic laziness perpetuated a mistake that could have continued for another 180 years if Najer et al. (2020) had not decided to examine the London syntype and discovered that there was a problem with its identity.

A large part of the blame for this problem must of course be laid at the feet of Jadwiga Złotorzycka, who redescribed and illustrated *Ph. reguli* three times in less than two decades without ever consulting type specimens or, apparently, the original description and illustration. Instead, her adherence to Fahrenholz's rule and the Eichlerian methodology (*sensu* Gustafsson & Najer 2022) made her assume that any and all specimens of *Philopterus* collected from *R. regulus* must be *Ph. reguli*. That is, because the *type host* of *Ph. reguli* is *R. regulus*, she assumed that the *natural host* of *Ph. reguli* is *R. regulus*. The only way to ascertain whether a type host is also the natural host is to compare specimens from multiple collections from that host with the holotype (or equivalent). This was not done, or it would have been discovered already in the 1960s that the London syntype was not conspecific with the species whose natural host is *R. regulus*.

Any subsequent researchers who identified their specimens – implicitly or explicitly – based on the redescriptions of *Ph. reguli* by Złotorzycka may be partially forgiven for acting in good faith, assuming that Złotorzycka's description was accurate. If the Brno species is the only *Philopterus* species naturally occurring on *R. regulus* in Europe, and that species is the one illustrated by Złotorzycka (1964b, 1977), then fresh collections that correspond to Złotorzycka's illustrations would reinforce the impression that her illustrations depict the correct species.

However, the fact that multiple researchers have drawn the wrong conclusion does not automatically mean that that conclusion should be retroactively validated when this is revealed. The name "*Philopterus reguli* Denny, 1842" does not refer to any and all specimens of *Philopterus* that are found on the type host of this species. Instead, in the absence of a validly designated neotype, the name *Ph. reguli* applies strictly, precisely, and exclusively to the specimen(s) that can reasonably be said to have been considered type specimens by Denny at the time of the publication of his monograph, as well as any specimens considered conspecific with these based on intrinsic characters. To put it more generally, specific names do not apply to hypothetical concepts of what a researcher believes they are dealing with, nor to hypothetical concepts of what they believe another researcher was dealing with.

This is precisely what makes judgements on whether designating a neotype for *Ph. reguli* that corresponds with the Brno species so difficult. Rewarding impreciseness and laziness for the sake of formality and expedience is, in principle, deleterious to the study of chewing lice. There is of course appeal in retaining the name *Ph. reguli* to the species of *Philopterus* that occurs on *Regulus regulus*, especially as that has been assumed to be the case for 180 years. However, in the overview of the history of the use of this name above (and in Table 3), I cannot see that changing the names would cause such a catastrophic upheaval in louse taxonomy, that it is worth doing. In almost all cases, the name is used as just a name in a list of species collected in or known from a region, with almost no significant extra information added to the original description in almost 180 years, until Najer et al. (2020) added more data under a different name.

In short, I do not agree with Mey (2020) that "stability and universality is threatened" to any significant degree by following the taxonomic recommendations published by Najer et al. (2020). Naturally, other researchers may evaluate the published data differently, and more opinions on this topic would be welcomed, especially if, as suggested by Mey (2020), the Commission needs to be called upon to settle this matter.

GOING FORWARD

There is no doubt that additional cases similar to this one may be discovered in the future. As a general rule of thumb, any louse publication that includes new taxa where there are not clear, complete illustrations, detailed descriptions, and comparisons with other taxa in the same group may be suspected of harboring parallel cases to *Philopterus reguli*. This is not least the case with older authors such as Burmeister, Denny, Giebel, Piaget, Kellogg, Mjöberg, Uchida, and others, but also with authors who habitually omitted meaningful morphological data from their descriptions and assumed species limits based on host associations. Apart from Eichler and Złotorzycka, this may include any author contemporary with them who did not completely illustrate or describe their species. More work clearly needs to be done in the spirit of the four publications by Clay & Hopkins (1950, 1951, 1954, 1960), who systematically went through older publications and sorted out species identity and limits, and erected neotypes to stabilize the nomenclature of the louse species described between 1758 and 1818.

As such, the present case may be seen as a "community precedent", to examine how louse researchers should approach cases of mistaken identity in the future. It should be clear that the kind of detailed analysis that is necessary to sort out some of these issues may be substantial, but much of this can be avoided if decisions on taxonomy, typification, and identity are sorted out carefully *before* publication rather than after.

MISTAKES WERE MADE

There is no doubt that Najer et al. (2020) made several substantial mistakes in their study, which caused more subsequent problems than they solved. For instance, the London syntype was not described, illustrated, or photographed, which would have shown unequivocally that it is not conspecific with the Brno species. They mistakenly called the London syntype a holotype, when Denny used no such term, and Denny had access to multiple specimens. Najer et al. (2020) could have designated either the London syntype or the Figure 4 specimen as the lectotype, thus simplifying the case considerably as the identity of *Philopterus reguli* would then have been unequivocal. They could also have designated any of the specimens they examined of the Brno species as the neotype of *Ph. reguli* and recommended that any previous name-bearing types were set aside by request to the Commission.

Similarly, Mey (2020) was too hasty to assign a neotype without analyzing the case adequately. This has caused problems with the neotype designation that invalidates it. In particular, the neotype designation violates the following Articles of the Code:

75.3.4 – a valid neotype designation needs to include "the author's reasons for believing the name-bearing type specimen(s) […] to be lost or destroyed, and the steps that had been taken to trace it or them". This was not included by Mey (2020), who merely asserted that "[a] part from the doubtful individual mentioned above [i.e., the London syntype], nothing of the original material of *Philopterus reguli* Denny has apparently been preserved". This is not known; moreover, it has not been established that the London syntype is not a genuine syntype. No attempts to trace other specimens were detailed by ether Najer et al. (2020) or Mey (2020); however, I could easily find a potential location of additional syntype specimens in the Jenyns collection, which may still be extant at the Museum of Zoology, Cambridge, UK (see above).

75.3.5 – a valid neotype designation needs to include "evidence that the neotype is consistent with what is known of the former name-bearing type from the original description and from other sources". This is clearly not the case. Not only is the Halle neotype morphologically different from the London syntype, but even if the syntype status of this specimen is dubious, the Halle neotype is also different from the Figure 4 specimen (Table 2), which is the only specimen we can tell for certain is (or was) a syntype. Mey (2020) stated that "Denny's copper engraving […] is at least consistent with the habitus of *P. reguli* as we know it today", but this is not true, as the Figure 4 specimen is drawn without *pronotal submarginal setae* and without trabeculae, both of which are clearly present in both the Brno species and the Halle neotype.

75.3.6 – a valid neotype designation must come "as nearly as practicable from the original type locality […] and, where relevant, from the same […] host species as the original name-bearing type". This is clearly not the case. Denny's description does not include any locality data for any of the specimens of *Ph. reguli* he examined, but his monograph is on species of lice from Great Britain, and his correspondent L. Jenyns mainly collected specimens in the Cambridge area (Suarez Ferreira 2021). In contrast, the Halle neotype is from northern Germany.

While there seems to be little genetic variation among the Brno species collected from Czech Republic and the Azores, there is some variation (Najer et al. 2020, 2021); moreover, specimens from Great Britain have not been analyzed. It is therefore not established that the population of *Philopterus* that naturally occur on *R. regulus* in Great Britain is conspecific with that of the continent, although this is of course exceedingly likely.

These three aspects alone are sufficient to consider the neotype proposed by Mey (2020) invalid, regardless of the identity of the London syntype and the Figure 4 specimen, and regardless of issues of stability of nomenclature. Following Article 75.4, this means that if the louse community decide that a neotype of *Ph. reguli* is the best way to go forward, the choice of a neotype is not limited by Mey (2020), as his neotype was not validly designated in accordance with Article 75.3.

RECOMMENDATIONS

Following this discussion, I would like to recommend the following guidelines :

1. Do not conflate "type host" with "natural host". In essence, "type host" is a taxonomic concept which is more or less only relevant in taxonomic papers where issues of neotype selection are or may be concerned. In almost all cases when discussing, for example, behaviour, ecology, evolution, phylogenetics, or life history of lice, the term that should be used is "natural host", which is the only biologically relevant one.
2. Do not assume louse identity based on host associations, but consult published descriptions, illustrations, photos, or keys, or confer with other experts who may be able to identify specimens. Enough data has been published in the last few decades to show that lice may be generalists, that straggling and host-switching occurs, and that host associations may not be reliable (summarized by Gustafsson & Najer 2022). Fahrenholz's rule and the Eichlerian methodology are invalid methods for species identification and should be discarded in favour of examination of intrinsic characters of the lice themselves.
3. Be clear and explicit about how each species collected or examined was identified and be clear and explicit about when there is reason for doubt about the species identity. In faunal lists, the sources (keys, descriptions, illustrations, museum specimens) that have been consulted should ideally be listed individually for each genus or species, so that there is no mistake about the level of certainty in the identification. If no published accounts of a species are adequate for identification, specimens may be identified to genus level only. Alternatively, it may be stated that specimens are tentatively identified by host association, but that a revision of the group is necessary. Whenever possible, consult experts in identification if there are any doubts at all.
4. Do not publish accounts of, for example, phylogenetics, life-history, ecology, or behaviour of lice without detailing how these lice were identified. If they cannot be reliably identified, do not use species-level names but confine your study, analysis and discussion to taxonomic levels that can be identified (e.g., genus level).
5. Whenever there is doubt about the identity of an older name you come across, consider devoting some time to analyzing the matter in detail, and perhaps track down any remaining types, examine them, and revise the species (or group) so that future researchers may benefit from your observations. Taxonomy, including revisionary taxonomy, is easier than commonly perceived, and needs input from more people.
6. If doing taxonomic work, make sure your taxonomic decisions follow the Code, and do not create additional unnecessary work for future taxonomists. In particular, when dubious cases of identity are discovered, great care must be taken not to cause more problem than necessary. Describing new louse species from hosts that are type hosts of congeneric louse species must be approached very carefully, and if there is the slightest doubt about the identity, it may be better to clarify the identity of the older names before publishing new names.

THE NAME OF THE LOUSE ON *R. REGULUS*

So, which name should be used for the species of *Philopterus* that evidently lives on *Regulus regulus* and *Regulus ignicapilla* across much of the range of these species?

For a start, the name of this species cannot presently be said to be *Philopterus reguli*. Based on our current knowledge, it seems likely that the description and illustration of *Ph. reguli* published by Denny (1842) refers to the Figure 4 species, whereas the only known extant supposed syntype associated with this name is the London syntype. Neither of these species has been shown to be conspecific with the species that naturally occurs on *R. regulus* and *R. ignicapilla*, which is the Brno species. Moreover, regardless of the identity of these specimens, the Halle neotype was not validly designated, and thus the taxonomic acts of Mey (2020) do not imply that the name *Philopterus reguli* should henceforth be used for the Brno species.

Going forward, as things stand today, the name *Ph. gustafssoni* must be used for the Brno species, as this is the only name for this species for which a validly designated name-bearing type is unequivocally designated. At the same time, the name *Philopterus reguli* must for the present be considered a *nomen dubium* (i.e., “a name of unknown or doubtful application”; the Glossary of the Code), as neither of the known specimens associated with this name (the London syntype and the Figure 4 specimen) can unequivocally be considered conspecific with the Brno species.

However, as the arguments on stability of nomenclature can only be settled by the louse community as a whole, and has no clear, unambiguous solution beyond an application to the Commission, this may change if it is felt that a neotype needs to be validly designated to retain the usage of *Ph. reguli* for the Brno species. This would depend on whether the community considers that the change from *Ph. reguli* to *Ph. gustafssoni* for the Brno species would cause too much instability to be warranted. Personally, I am not presently convinced that that is the case, but this may change if better and more extensive arguments are put forward that those presented by Najer et al. (2020) and Mey (2020).

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Small non-volant mammals of the Provincia de El Oro, Ecuador: results of a field survey and annotated checklist

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[6] urn:lsid:zoobank.org:author:BEC9757B-39B7-49E2-9D6A-C073916597EF
[7] urn:lsid:zoobank.org:author:FDC850C2-EA35-4BF2-9302-2AE61E782F50

Abstract. From 2015 to 2022 we sampled small (< 1 kg) non-volant mammals in most regions of the Provincia de El Oro in southwestern Ecuador. A total of 228 individuals belonging to 37 species were collected and recorded. Based on a complete account of this collection, supplemented by additional museum specimens and reliable literature reports, we present an annotated checklist including the 46 species of small non-volant mammals currently known from Provincia de El Oro. The compilation provided represents one of the most comprehensive data sets on non-volant mammals collected from southwest Ecuador. A gazetteer of the collection localities of all specimens is provided and some taxonomic and biogeographical issues are discussed. Ten of the registered species (22%) are in some category of threat in Ecuador: eight are Vulnerable (VU), one is Endangered (EN), and one is Critically Endangered (CR). The record of the Water Mouse *Neusticomys orcesi* (Jenkins & Barnett, 1997) corresponds to the second locality for this rodent, while also representing the lowest altitudinal record (2,000 m a.s.l.). Shrub and herbaceous and native forest vegetation are the most fragmented habitats, with 2,546 and 2,403 patches, respectively. In addition, these ecosystems concentrate the highest species richness, including endemic and endangered species. The present report establishes a baseline for future inventory efforts in the west of Ecuador. Such basic information is essential for natural resource management and conservation to be successful.

Key words. Diversity, fragmented ecosystems, *Neusticomys orcesi*, piedmont forest, montane forest.

INTRODUCTION

The tropical Andes of South America are one of the most biodiverse regions of the planet, with high levels of endemism (Myers et al. 2000; Voss 2003; Ceballos & Ehrlich 2006; Prado et al. 2014; Sklenář et al. 2014; Patton et al. 2015), and where several globally threatened species are concentrated (Amori et al. 2013). Despite this, study efforts and vouchers are poorly represented in publications and museum collections (Patton et al. 2015).

Several papers have been published in an attempt to fill information gaps in the Andes of Ecuador, such as in the Andean areas of the provinces (from north to south): Carchi (Tirira & Boada 2009; Ojala-Barbour et al. 2019), Imbabura (Lee et al. 2010; Curay et al. 2022), Pichincha (Curay et al. 2019), Napo (Voss 2003; Lee et al. 2006, 2008), Cotopaxi (Jarrín-V 2001; Lee et al. 2022), Morona Santiago (Lee et al. 2011; Brito & Ojala-Barbour 2016), and Azuay (Barnett 1999). In the Provincia de El Oro, although the first mammal studies were conducted in the early 20th century (Anthony 1921, 1923, 1924a, 1924b, 1926), few subsequent works have been carried out (Baker et al. 2009; Carrera et al. 2010; Velazco & Patterson 2014; Brito & Valdivieso-Bermeo 2016; Torres-Porras et al. 2017; Brito et al. 2018, 2022).

We define small non-volant mammals as all those species whose mass ranges below 1 kg when adult, which includes most rodents, Eulipotyphla, and also various marsupials, some primates, lagomorphs, and carnivores (Patton et al. 2015; Wilson et al. 2005, 2017). As a result of our field surveys in the Provincia de El Oro between 2015 and 2022, here we provide a checklist of 46 species of small non-volant mammals, complemented with specimens preserved in national natural history museums and

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literature. This report is intended to establish a baseline for future inventory efforts in western Ecuador.

MATERIAL AND METHODS

Study area. The Provincia de El Oro is in the southwestern region of Ecuador (Fig. 1). Part of the province is crossed by the western Andes, while the majority corresponds to the coastal region (Garzón-Santomaro et al. 2019a).

In the Provincia de El Oro, the tropical rainforests of the Chocó biogeographic region (coastal tropical rainforest) and the dry equatorial forest of Tumbes (coastal tropical dry forest) are found together. El Oro is the Ecuadorian province where the Andes are closest to the sea (ca. 20 km), with an altitudinal gradient between 0 and 3,900 m a.s.l. (Garzón-Santomaro et al. 2019a).

Data collection. From 2015 to 2022 we sampled 20 localities, trying to cover most of the ecosystems of the Provincia de El Oro. The mammals were captured with Sherman-like traps (7.5 × 9 × 29 cm), and Tomahawk-like

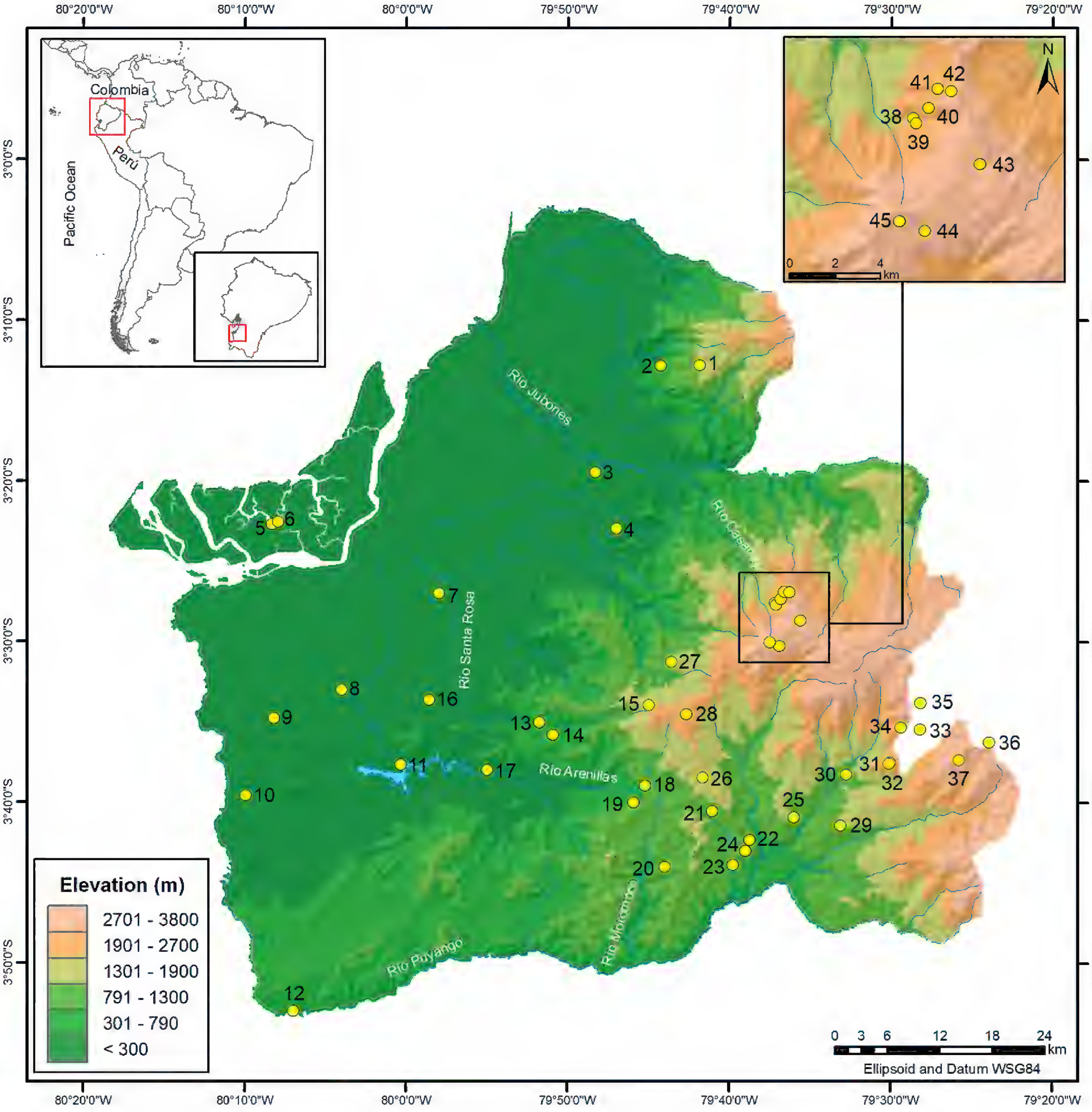

Fig. 1. Map Provincia de El Oro showing localities from which materials were recorded. Details of the numbered localities are shown in Table 1.

Table 1. Locations indicated in the text and in Fig. 1.

Number	locality	latitude	longitude	altitude	source
1	El Retiro	-3.213330	-79.697777	1,690	Brito et al. (2018)
2	Cascadas de Manuel	-3.213610	-79.737777	345	Brito et al. (2018)
3	Pasaje	-3.324400	-79.805318	29	Weksler (2006)
4	Pasaje. La loma	-3.382390	-79.783416	80	Ramírez-Jaramillo (2019)
5	Jambeli	-3.378480	-80.139130	5	Orihuela-Torres et al. (2019)
6	Las Casitas. Jambeli	-3.375830	-80.132500	1	Orihuela-Torres et al. (2018)
7	Santa Rosa	-3.450000	-79.966660	100	Rossi et al. (2010); Weksler & Lòss (2015)
8	Los Pozos	-3.550000	-80.066670	50	Tribe (2015)
9	Reserva Ecológica Arenillas	-3.579720	-80.136944	45	Brito et al. (2018)
10	Arenillas. El Cubo destacamento	-3.659990	-80.165830	112	this study
11	Tahuin	-3.627770	-80.005830	132	Brito et al. (2018)
12	Puyango	-3.883333	-80.116600	350	Rossi et al. 2010; this study
13	El Guayabo	-3.583600	-79.862520	550	this study
14	Sabayan	-3.596517	-79.848960	478	this study
15	El Biron	-3.565833	-79.750020	1,835	Brito et al. (2018)
16	El Biron Alto	-3.560640	-79.976844	1,651	this study
17	Piedras	-3.633330	-79.916660	300	Voss (1992)
18	Reserva Buenaventura	-3.649160	-79.753611	543	Torres-Porras et al. (2017)
19	Cresta Polo	-3.666660	-79.765550	979	this study
20	Moromoro	-3.733333	-79.733333	1,060	Brito et al. (2018)
21	Piñas	-3.675413	-79.684280	1,100	Anthony (1922)
22	San Patricio	-3.705277	-79.645830	811	this study
23	San Roque	-3.731256	-79.662694	930	this study
24	Portovelo	-3.716666	-79.650000	609	Anthony (1921)
25	Zaruma	-3.681935	-79.599977	1,150	Anthony (1921)
26	El Chiral	-3.641000	-79.694000	1,630	Anthony (1921)
27	Paccha	-3.520833	-79.726380	1,444	Brito et al. (2018)
28	Yacuviñay	-3.574999	-79.711389	2,410	this study
29	Güishiguiña	-3.690248	-79.551947	1,650	this study
30	Salvias	-3.637504	-79.545890	1,215	Weksler (2006)
31	Chivaturco	-3.625000	-79.501111	2,433	this study
32	Chivaturco. Cumbre	-3.626048	-79.501848	2,500	this study
33	Taraguacocha	-3.590884	-79.469717	3,277	Anthony (1921)
34	Sabadel	-3.588758	-79.489921	3,300	this study
35	Cerro de Arcos	-3.550830	-79.478333	3,668	this study
36	Laguna de Chinchilla	-3.603861	-79.398778	3,664	this study
37	Via Salvias-Zaruma	-3.622521	-79.429915	1,899	Weksler (2006)
38	Gallo Cantana	-3.459450	-79.619840	2,053	this study
39	Cabecera del Rio Casacay	-3.461667	-79.618717	2,003	this study
40	Ashigsho. vía a Gallo Cantana	-3.455410	-79.613760	2,489	this study
41	Ashigsho. Rancho Triste	-3.447850	-79.610150	2,539	this study
42	Ashigsho. Tanque	-3.448720	-79.604900	2,801	this study
43	Shiñinguro	-3.477778	-79.593333	3,169	this study
44	Payana	-3.504444	-79.615278	3,141	this study
45	Chillacocha	-3.500556	-79.625278	3,338	this study

Table 2. Collecting localities of small non-volant mammals in Provincia de El Oro (our study).

number	locality	traps / night	n° specimens	n° species
12	Puyango	300	6	3
13	El Guayabo	1,200	10	5
14	Sabayan	1,200	16	5
16	El Biron Alto	600	7	1
19	Cresta Polo	300	6	2
22	San Patricio	200	3	1
28	Yacuviñay	300	20	3
31	Chivaturco	200	2	2
32	Chivaturco. Cumbre	200	16	4
34	Sabadel	150	5	3
35	Cerro de Arcos	150	12	6
36	Laguna de Chinchilla	150	17	6
38	Gallo Cantana	150	26	4
39	Cabecera del Rio Casacay	80	5	4
40	Ashigsho. vía a Gallo Cantana	150	13	4
41	Ashigsho. Rancho Triste	600	28	6
42	Ashigsho. Tanque	150	7	3
43	Shiñinguro	200	5	2
44	Payana	200	12	6
45	Chillacocha	350	12	5
Total		**6,830**	**228**	**25**

traps (14 × 14 × 40 cm), which allowed for 6,830 trap-nights. The traps were arranged in linear sampling transects, with two traps per station, combining a Sherman and a Tomahawk trap, with a separation of approximately 10 m between stations. The bait consisted of a mixture of oats with vanilla and coconut essence (Brito & Ojala-Barbour 2016). For the handling and care of the specimens, the recommendations of Sikes et al. (2016) were followed. Vouchers were deposited at the Instituto Nacional de Biodiversidad, Quito, Ecuador (MECN; formerly known as Museo Ecuatoriano de Ciencias Naturales), and Museo Escuela Politécnica Nacional (MEPN), Quito, Ecuador.

Identification, checklist structure and presentation. Taxonomic identification of rodents was based on Patton et al. (2015), Pardiñas et al. (2017), and Brito et al. (2022); marsupials based on Ojala-Barbour et al. 2013), Astúa (2015), and Patterson (2016); shrews based on Zeballos et al. (2018); and rabbits based on Ruedas et al. (2019). In all cases they were also compared with museum specimens.

The updated list of 46 known small non-volant mammals in El Oro is organized according to taxonomic rank following Wilson & Reeder (2005), for squirrels we follow de Vivo & Carmignotto (2015), and Abreu-Júnior et al. (2020). Details of our collection localities, as well as those reported in the literature, are listed in Table 1, and the sampling effort at each locality is provided in Table 2. The compendium contains the locality of the record for each species, a brief identification, and museum material. It also details new records, and taxonomic and/or natural history comments for each species inhabiting the Provincia de El Oro. Finally, for the conservation status at the global level we followed the IUCN (2021), and at the national level we followed Tirira (2021).

Landscape fragmentation and diversity. Currently there is a wide availability of geospatial data that allows explanation of the relationships of species with the landscape. We obtained the land cover and land use of the Provincia de El Oro at a scale of 1:25 000 from 2015 (official mapping at the best scale) produced by the Ministerio de Agricultura y Ganadería de Ecuador (MAG 2009-2015). With these data we calculated eight composition metrics and one landscape configuration metric (Table 3), and to estimate the species richness present in each landscape we used information from 45 localities (Table 1).

The land cover and land use format of the Provincia de El Oro was transformed from shapefile (.shp) to raster

Table 3. Landscape fragmentation metrics in the Provincia de El Oro.

metric	native forest	páramo	shrub and herbaceous vegetation	agricultural land	unit
class area	1,323	129	662	3,000	km^2
number of patches	2,403	31	2,546	1,648	–
patch density	1.82	0.24	3.85	0.55	number per 100 hectares
mean of contiguity index	0.88	0.57	0.9	0.91	-
largest patch index	11.8	62.7	19	27.2	percentage
landscape division index	0.97	0.47	0.95	0.85	proportion
aggregation index	97.3	98.9	96.9	98.5	percentage
fractal dimension index	1.14	1.14	1.13	1.12	–

(.tif) with a spatial resolution of 7.5 meters to calculate landscape metrics. The data were processed using QGIS 3.16.6 Hannover software. Using the R landscapemetrics package for categorical map patterns, eight metrics proposed in Hesselbarth et al. (2021) were calculated to estimate the degree of landscape fragmentation (Native Forest, Páramo, Shrub Vegetation, Herbaceous Vegetation and Agricultural Land). The interactions between patches within the mosaic were also calculated, since these elements, by influencing the ecological characteristics of the species, can be a tool for defining conservation strategies (McGarigal et al. 1995).

RESULTS

We recorded a total of 320 specimens belonging to 37 species, of which 228 specimens were collected as vouchers. Nine additional species occur in the Provincia de El Oro, including one species from previous collections preserved in Quito and eight species reported in the literature. Altogether, the total number of small non-volant mammal species currently known from the province of El Oro is 46 (see taxonomic accounts). Six species are endemic to Ecuador (13%). Ten of the species (22%) are in some category of threat in Ecuador (Tirira 2021), eight are Vulnerable (VU), one is Endangered (EN), and one is Critically Endangered (CR).

Our results show that the main landscape matrix of the Provincia de El Oro is agricultural land (Fig. 2A), occupying 3,000 km^2 (51.8% of the total area of the province) and harboring 23 species of small non-volant mammals. The native forest (26 spp., and 4 endemics) has an area of 1,323 km^2, which is equivalent to 22.84% of the province and is structured by 2,403 patches, with a patch density of 1.82 per 100 hectares, where the index of the largest patch has a value of 11.8%. In addition, the division index obtained was 0.97 indicating that the native forest fragments are scattered and tend to be isolated within the landscape matrix. While the shrub and herbaceous vegetation (23 spp., and 2 endemics) has an area of 662 km^2 made up of 2,546 patches with a density of 3.85 per 100 ha where the largest patch has a value of 19% showing that it has a higher degree of fragmentation in relation to native forests.

Taxonomic accounts

Order Didelphimorphia Gill, 1872
Family Didelphidae Gray, 1821

Caluromys derbianus (Waterhouse, 1841)

Material. 1 specimen collected (MECN 492).

Locality. San Roque (23).

Identification. Dorsal coat reddish brown, ventral color yellowish white. Head light gray, with a dark brown stripe in the center of the face. Ears hairless. Prehensile tail 30–50% wooly at its base, while tip of tail bare and whitish.

Conservation status. National, Vulnerable (VU); Global, Least Concern (LC).

Chironectes minimus (Zimmermann, 1780)

Material. None.

Literature records. Moromoro (Brito et al. 2018).

Identification. Silver-gray dorsum with four broad bands running laterally across the dorsum, these are blackish in color. The pattern of its coloration makes it distinguishable from all other opossums. The hind legs have an interdigital membrane up to the end of each phalanx (Astúa 2015).

Conservation status. National, Near Threatened (NT); Global, Least Concern (LC).

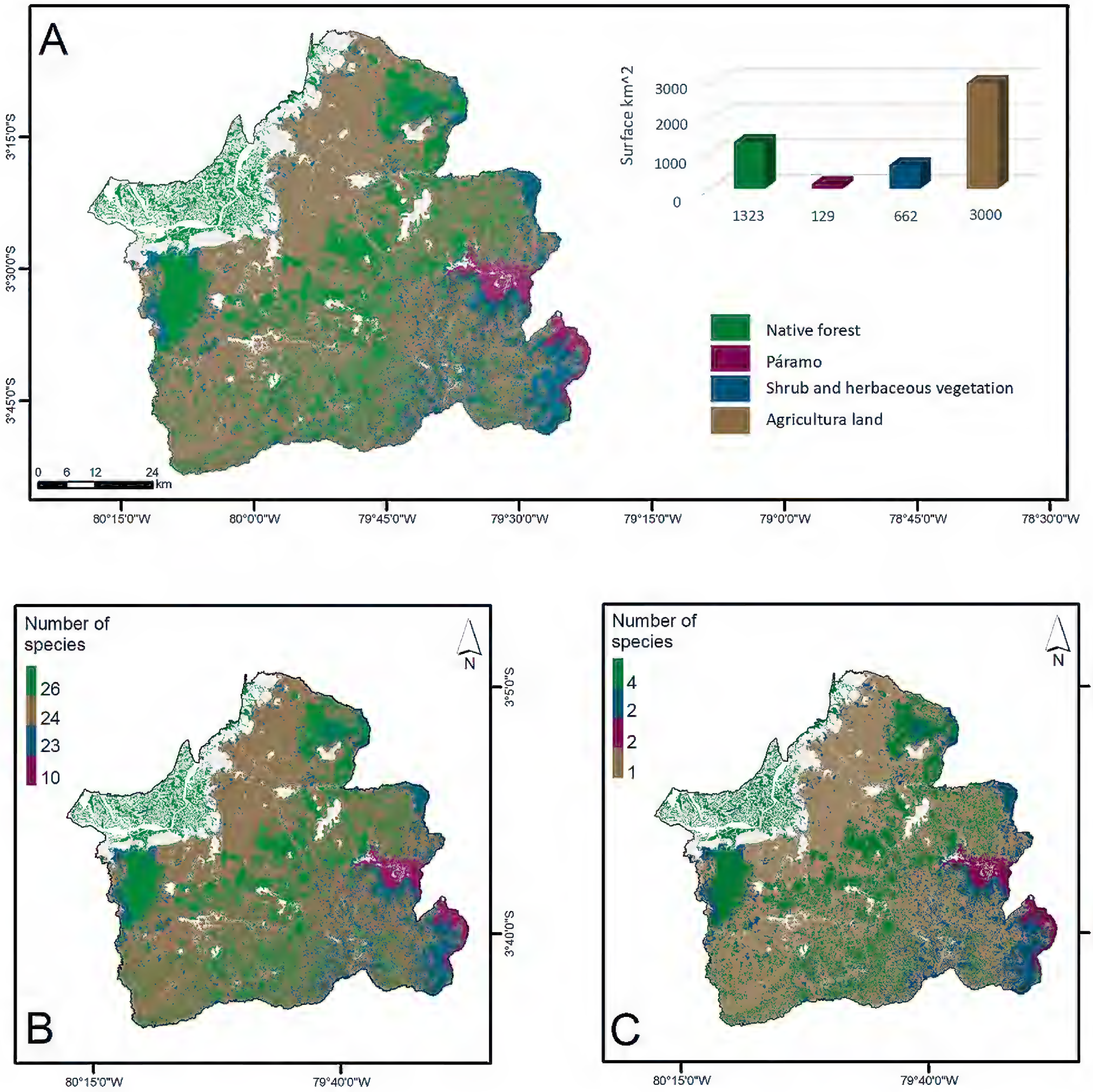

Fig. 2. **A**. Land cover in the Provincia de El Oro. **B**. Species richness by land cover. **C**. Species endemism by land cover.

Didelphis marsupialis Linnaeus, 1758

Material. None.

Localities. Cascadas de Manuel (2), Reserva Ecológica Arenillas (9), Tahuin (11), Puyango (12), Cresta Polo (19), San Patricio (22).

Literature records. Reserva Buenaventura (Torres-Porras et al. 2017).

Identification. Dorsum with pale yellow hairs interspersed with black hairs. Ears large and black (Fig. 3A). Tail naked, black at its base and white at its tip.

Conservation status. National and Global, Least Concern (LC).

Didelphis pernigra J. A. Allen, 1900

Material. None.

Localities. Biron Alto (15), Yacuviñay (28), Sabadel (34), Cerro de Arcos (35), Laguna de Chinchilla (36), Ashigsho, vía Gallo Cantana (40), Ashigsho, Tanque (42), Shiñinguro (43), Payana (44), Chillacocha (45).

Identification. Dorsum is black to deep gray. White head with a black mask that starts at the nose and goes behind the eyes and extends faintly to the base of the ears. The ears are pink or black but have white tips (Astúa 2015).

Conservation status. National and Global, Least Concern (LC).

Marmosa isthmica Goldman, 1917

Material. None.

Literature records. Santa Rosa and Puyango (Rossi et al. 2010).

Identification. Dorsal dark brownish to pale brown, with the sides of the body slightly paler. Tail is long (approximately 130% of the head-body length), and the proximal 10% is covered with hair. Ventral is yellowish beige to orange from chin to anus, with the hairs on the sides having a yellowish gray to orange base (Astúa 2015).

Conservation status. National: Least Concern (LC); Global: Not evaluated.

Marmosa perplexa Anthony, 1922

Material. None.

Literature records. Piñas (Anthony 1922; Voss & Giarla 2021).

Identification. The second upper premolar (P2) has an incomplete lingual cingulum. The postprotocrista of upper third molar (M3) is short (terminating at or near the base of the metacone), and lower molars (m1–m3) lack posterior cingulids (Voss & Giarla 2021).

Conservation status. National, Vulnerable (VU); Global, Not evaluated.

Remarks. With type locality in Ecuador: Trail from Zaruma to Loja near Punta Santa Ana, 3650 feet (1113 m) above sea level, in the western Andean foothills of Loja province, Ecuador (Anthony 1922).

Marmosa phaea Thomas, 1899

Material. 1 specimen collected (MECN 4869).

Locality. Puyango (12).

Identification. Dorsal color brown (Fig. 3B) and ventral color cream-orange. Tail long (141% of the head-body length), naked, and brown, with small white spots at its tip. Skull with sparsely developed crest (Voss et al. 2014), postorbital processes well developed, a complete lingual cingulum on upper second premolar (P2), and long postprotocristae (Voss & Giarla 2021).

Conservation status. National and Global, Vulnerable (VU).

Remarks. The locality of Puyango is the southernmost record of the species.

Marmosa simonsi Thomas, 1899

Material. 1 specimen collected (MECN 6036).

Localities. El Guayabo (13).

Literature records. Puyango (Gutiérrez et al. 2010; Rossi et al. 2010).

Identification. Dorsal color is grayish. There is no midline on the face as in some congeners. The tail is long (approximately 121% of the head-body length), and the most proximal 10% is covered with hair. Ventral hair is yellowish (Fig. 3C), with the hairs on the chest, abdomen and inner part of the limbs with a gray base (Astúa 2015).

Conservation status. National, Near Threatened (NT); Global, Not evaluated.

Remarks. With type locality in Ecuador: Puná Island, Guayas, Ecuador (Thomas 1899).

Marmosops caucae (Thomas, 1900)

Material. 6 specimens collected (MECN 4635, 6948, 4675, 4682, 4684, 6975).

Localities. San Patricio (22), Cresta Polo (19), Ashigsho, vía Gallo Cantana (40).

Literature records. Portovelo (Díaz-Nieto et al. 2016).

Identification. Fur dense and short. Hair on back grayish brown (Fig. 3D). Ventral color yellowish white. Tail bare and bicolor. Skull without cranial ridges.

Conservation status. National and Global, Least Concern (LC).

Philander melanurus (Thomas, 1899)

Material. 2 specimens collected (MECN 5028, 5754).

Localities. Reserva Buenaventura (18), El Guayabo (13).

Literature records. Reserva Buenaventura (Curay et al. 2019), Cresta Polo and Reserva Ecológica Arenillas (Brito et al. 2018).

Identification. Dorsum blackish gray from head to tail. Head gray, with two whitish spots above eyes (Fig. 3E). Chin white. Phalanges of feet and hands pink.

Conservation status. National, Least Concern (LC); Global, Not evaluated.

Remarks. With type locality in Ecuador: Paramba, Rio Mira, Imbabura, Ecuador; alt. 1100 m (Thomas 1899).

Order Paucituberculata Ameghino, 1894
Family Caenolestidae Trouessart, 1898

Caenolestes caniventer Anthony, 1921

Material. 8 specimens collected (MECN 4811, 4812, 4830, 4841, 4900, 6933, 6938, 7018).

Localities. Yacuniñay (28), Ashigsho, Rancho Triste (41), Ashigsho, vía Gallo Cantana (40), Chillacocha (45), Payana (44).

Literature records. El Chiral (Anthony 1921; Ojala-Barbour et al. 2013).

Identification. Dorsum blackish brown. Ventral color grayish, with whitish hair tips that give it a grayish ap-

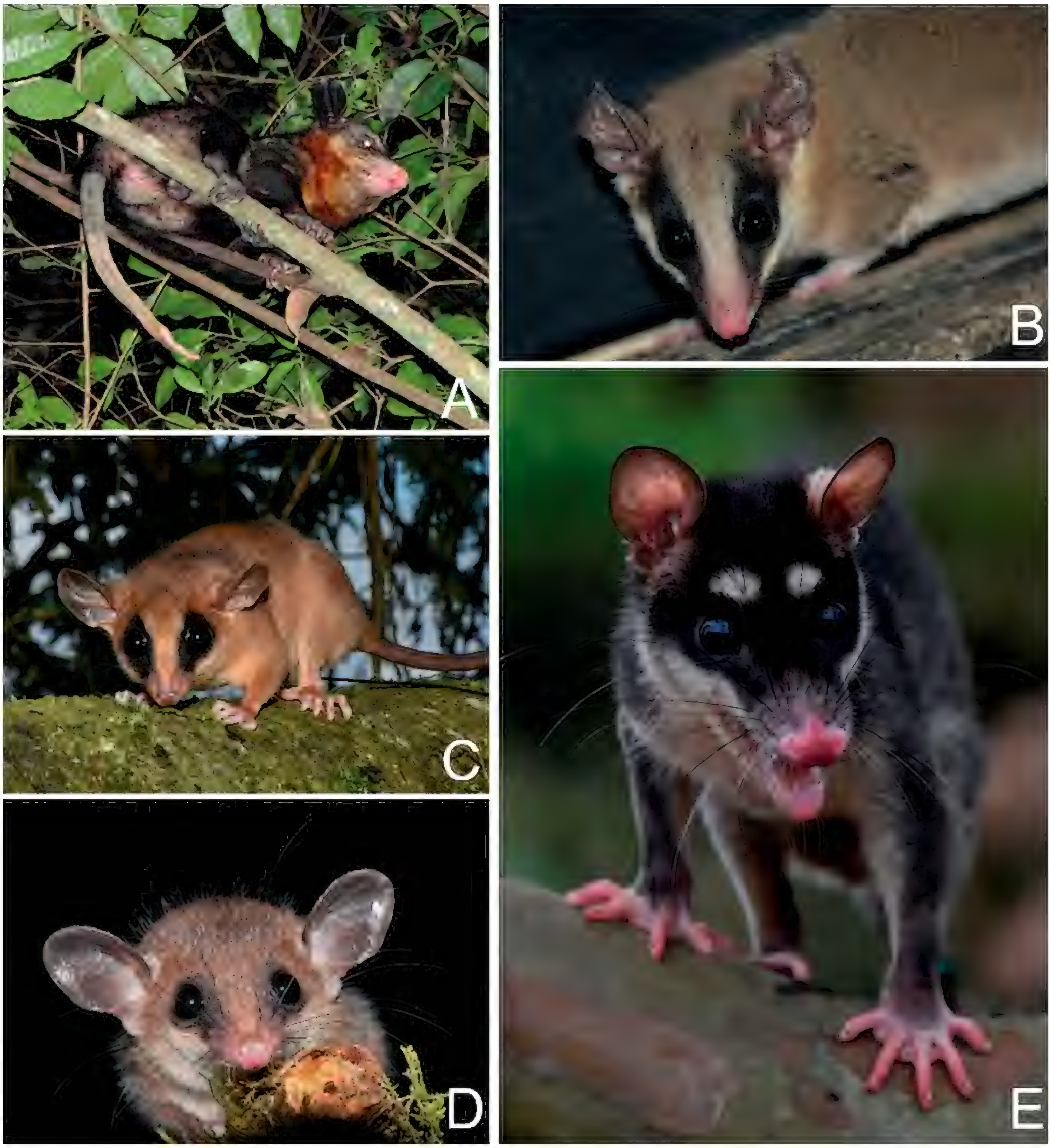

Fig. 3. Marsupials recorded in the Provincia de El Oro. **A**. *Didelphis marsupialis* recorded in the San Patricio. **B**. *Marmosa phaea* (MECN 4869) recorded in the Puyango. **C**. *Marmosa simonsi* (MECN 6036) recorded in the El Guayabo. **D**. *Marmosops caucae* (MECN 4635) recorded in the Cresta Polo. **E**. *Philander melanurus* (MECN 5754) recorded in the El Guayabo (Photos by J. Brito).

pearance (Fig. 4). Skull robust, resting on the bulla and canines (Fig. 5). Anterorbital vacuity open and post palatine foramen curved (Ojala-Barbour et al. 2013). Prongs 1.6 times longer than glans, relatively cylindrical and striated, progressively tapering to a hook-shaped distal tip (Brito et al. 2022).

Conservation status. National, Vulnerable (VU); Global, Near Threatened (NT).

Remarks. With type locality in Ecuador: “El Chiral, Western Andes; altitude, 5350 ft.; Prov. del Oro, Ecuador” (Anthony 1921:6).

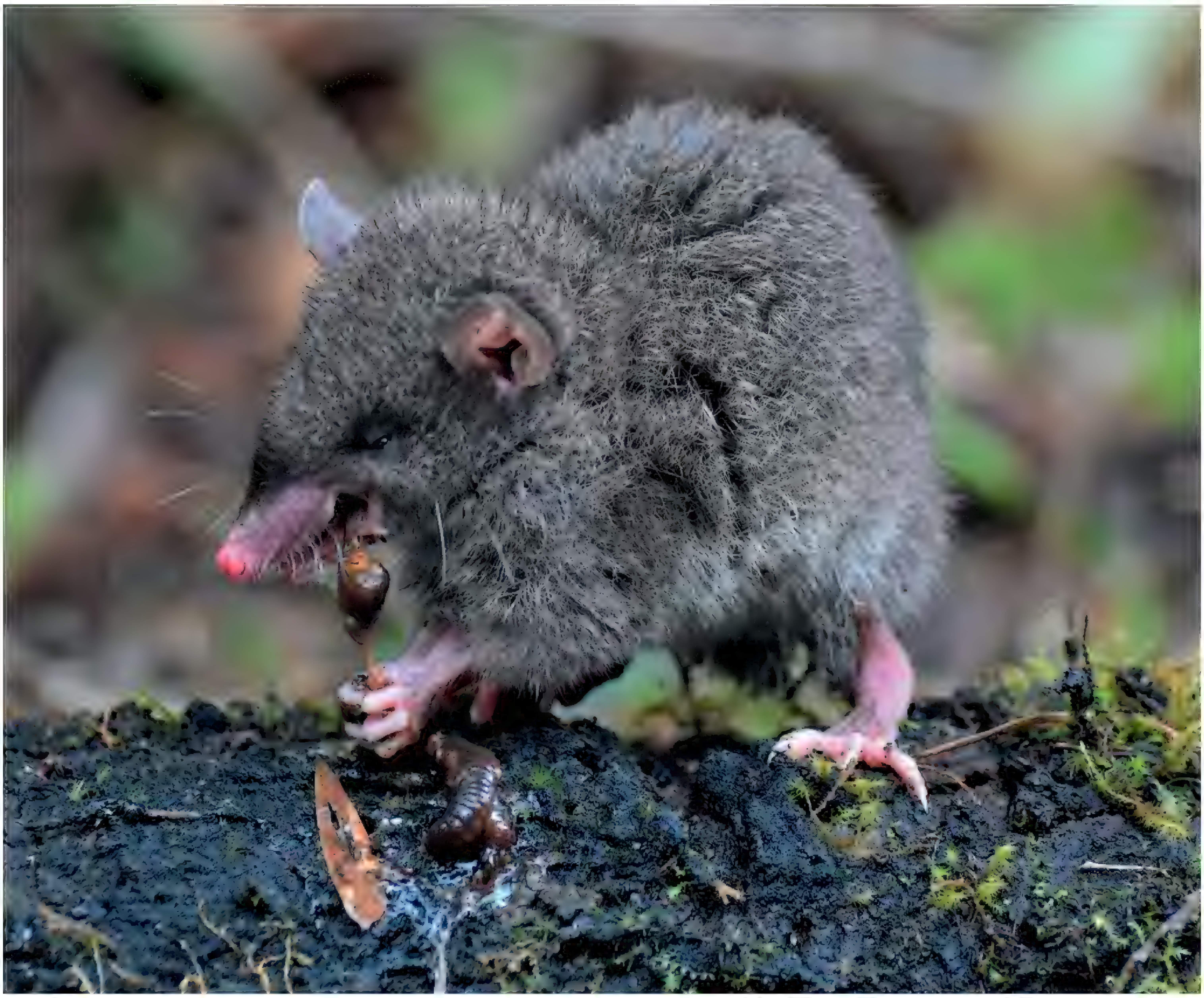

Fig. 4. Gray-bellied Shrew Opossum, *Caenolestes caniventer* (MECN 7018) recorded in the Ashigsho, Provincia de El Oro. (Photo by J. Brito).

Order Rodentia Bowdich, 1821
Family Sciuridae Fischer, 1817

Microsciurus simonsi Thomas, 1900

Material. None.

Localities. Sabayan (14), Biron Alto (16), Reserva Buenaventura (18).

Literature records. Cascadas de Manuel (Brito et al. 2018).

Identification. Dorsum dark brown with orange. Ears short and postauricular patches absent. Tail no longer than the body and not very bulky (Fig. 6A).

Conservation status. National, Vulnerable (VU); Global, Not evaluated.

Remarks. Species endemic to Ecuador, type Locality. "Porvenir, near Zaparal, Province of Bolivar, Ecuador. Altitude 1500 m" (Thomas 1900:294).

Simosciurus nebouxii (I. Geoffroy St.-Hilaire, 1855)

Material. 2 specimens collected (MECN 504, 6154).

Localities. San Roque (23), Puyango (12), Reserva Buenaventura (18), San Patricio (22), Reserva Ecológica Arenillas (9), El Guayabo (13), Sabayan (14).

Identification. Dorsum light gray, posterior part on the drupe pale yellow; conspicuous white to grayish-white nuchal patch (Fig. 6B). Feet and hands dark brown.

Conservation status. National, Least Concern (LC); Global, Not evaluated.

Syntheosciurus granatensis (Humboldt, 1811)

Material. None.

Localities. Cascadas de Manuel (2), Tahuin (11), Piñas (21), Chivaturco (31).

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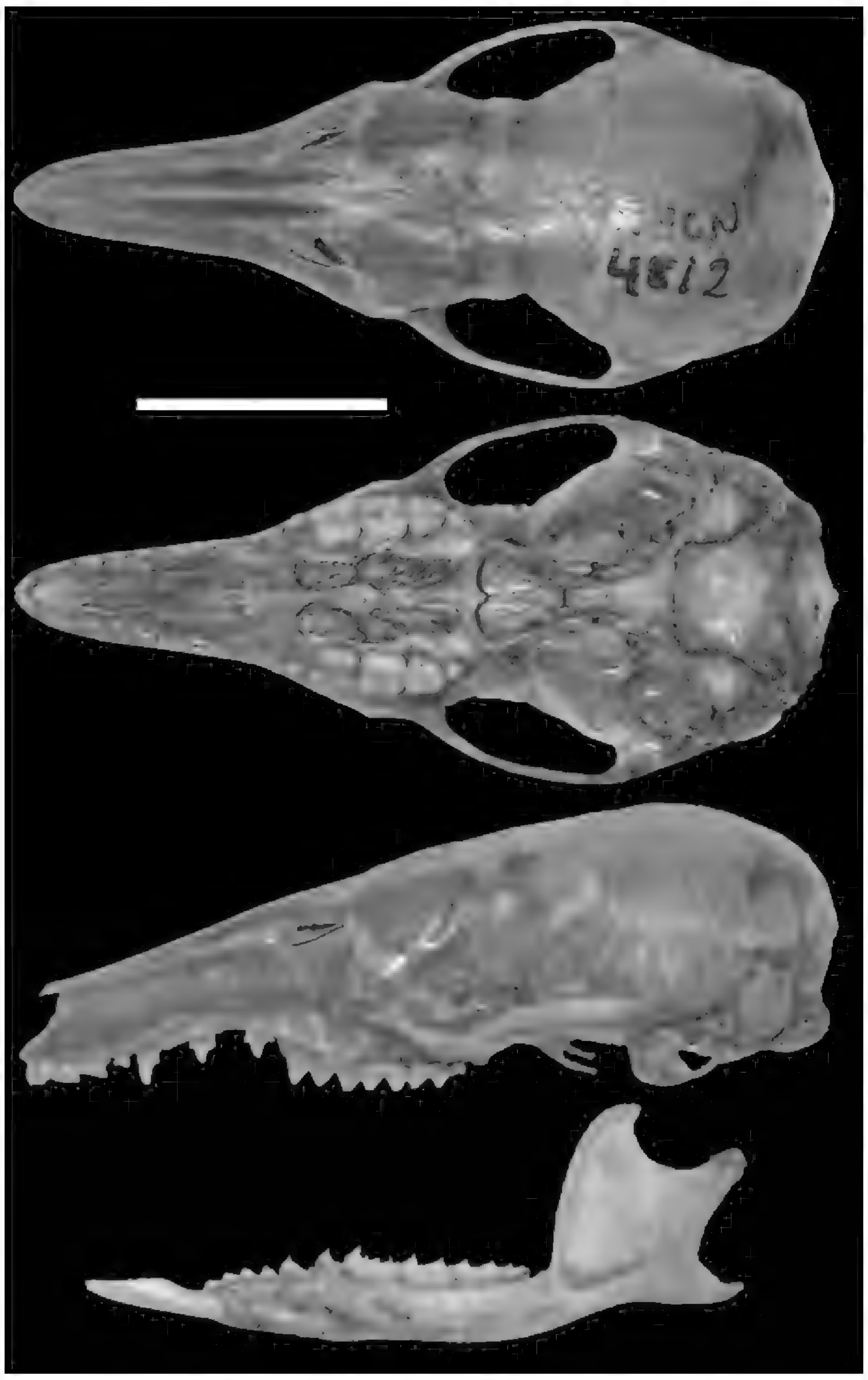

Fig. 5. Dorsal, ventral and lateral view of the skull of *Caenolestes caniventer* (MECN 4812) recorded in the Chillacocha, Provincia de El Oro. Scale 10 mm. (Photos by J. Brito).

Literature records. Pasaje, La Loma (Ramírez-Jaramillo 2019), Reserva Buenaventura (Torres-Porras et al. 2017).

Identification. Back and belly reddish, interspersed with brown. Tail thick, bulging, ochraceous proximally and blackish at tip (Fig. 6C). Ventral orange.

Conservation status. National and Global, Least Concern (LC).

Remarks. Ramírez-Jaramillo (2019) reported a specimen with leucism for the locality of Pasaje, La Loma.

Family Cricetidae Fischer, 1817

Aegialomys xanthaeolus (Thomas, 1894)

Material. None.

Localities. Reserva Ecológica Arenillas (9).

Literature records. Pasaje and Portovelo (Weksler 2006), and Jambelí (Orihuela-Torres et al. 2019).

Other specimens. MEPN 6069, 6070, 6500, 6503–6505, 6523, 6875.

Identification. Dorsal pelage color copper, weakly grizzled with brown; ventral pelage grayish cream; tail hirsute, longer than head body length (Prado & Percequillo 2017).

Conservation status. National and Global, Least Concern (LC).

Akodon mollis Thomas, 1894

Material. 55 specimens collected (MECN 4706, 4717, 4718, 4725–4727, 4783, 4800, 4808, 4831, 4833, 4845, 4847,4849, 4886, 4887, 4889, 4890, 4894, 4896–4899, 4908, 4909, 4911, 5755, 5758–5760, 5765–5767, 6826, 6930, 6931, 6934, 6944, 6945, 6947, 6980, 6983, 6984, 6990, 6994, 7007–7009, 7013–7016, 7019).

Localities. Biron Alto (16), Yacuviñay (28), Chivaturco (31), Sabadel (34), Laguna de Chinchilla (36), Cabecera del Río Casacay (39), Ashigsho, vía Gallo Cantana (40), Ashigsho, Rancho Triste (41), Ashigsho, El Tanque (42), Shiñinguro (43), Payana (44).

Identification. Dorsal pelage dark olive (Fig. 7A). Tail short, furred, distinctly to indistinctly bicolored, with darker hairs above. Skull stocky with robust rostrum; long incisive foramina extend posteriorly beyond anterior margin of M1s.

Conservation status. National and Global, Least Concern (LC).

Natural history: A pregnant female with three fetuses was recorded in March 2022, and four males with scrotal testicles were recorded in November 2015.

Chilomys neisi Brito, Tinoco, García, Koch & Pardiñas, 2022

Material. 1 specimen collected (MECN 6187).

Localities. Ashigsho, Rancho Triste (41).

Identification. Dorsal fur dark neutral gray; venter coat dark neutral gray. Periocular ring jet black (Fig. 7B). Postauricular patch present. Long tail unicolor fawn except for apex, which is white. Long nasal; zygomatic plate straight; M1 without anteromedian flexus; m1 without anteromedian flexus; hemal arches absent. Proodont upper incisors with orange and smooth front enamel; crested and pentalophodont molars, noticeably thick enamel (Brito et al. 2022).

Conservation status. Not evaluated.

Remarks. Species endemic to Ecuador, type Locality. Ecuador, Provincia de El Oro, Cantón Chilla, Ashigsho, −3.44785, −79.61015; elevation 2,539 m (Brito et al. 2022).

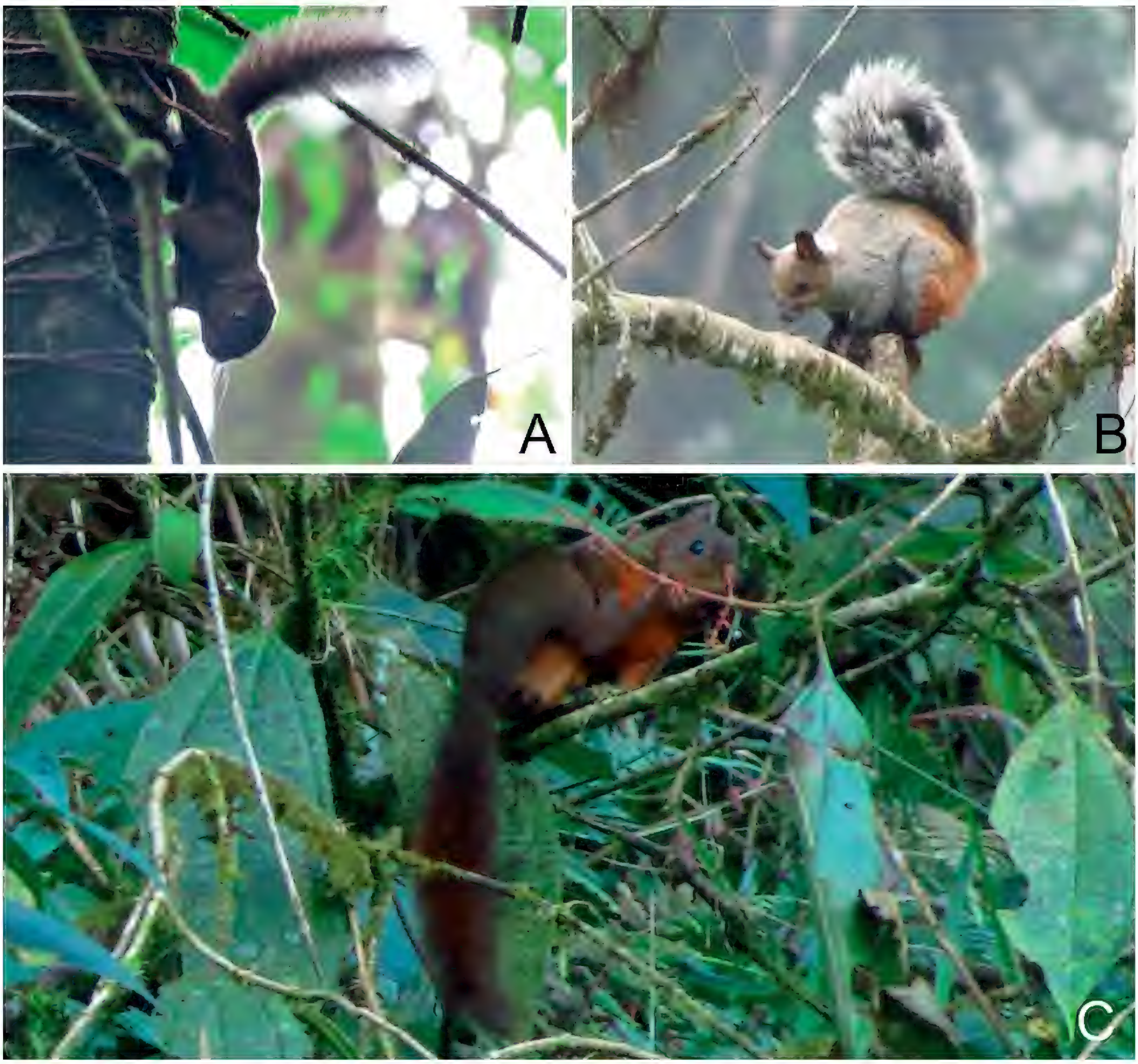

Fig. 6. Squirrels of the Provincia de El Oro. **A**. *Microsciurus simonsi* recorded in the Cascadas de Manuel. **B**. *Simosciurus nebouxii* recorded in the San Patricio. **C**. *Syntheosciurus granatensis* recorded in the Paccha (Photos by G. Pozo).

"*Handleyomys*" *alfaroi* (J. A. Allen, 1891)

Material. 13 specimens collected (MECN 4631, 4634, 4640, 5752, 5753, 5756, 5762–5764, 6149).

Localities. El Guayabo (13), Sabayan (14), Cresta Polo (19).

Identification. Small; head and body of adults 97–122 mm long, tail 103–122 mm, hind leg length 25–28 mm, ear length 16–19, weight 29–39 g. Dorsal coat dark reddish brown (Fig. 7C); sides ocher to orange; belly grayish white or yellowish white, always with gray hair base. Short fur (5–7 mm). Tail bicolor in the proximal half and then dark to the tip. Skull small with short rostrum; temporal crests poorly developed; wide interorbital region. Alisphenoid strut absent.

Conservation status. National and Global, Least Concern (LC).

Ecological notes. Three males with scrotal testicles were recorded in November 2018.

Taxonomic note. Annotated as "*Handleyomys*" because of its provisional allocation as a member of *Handleyomys* (see Weksler 2015).

Ichthyomys tweedii Anthony, 1921

Material. 1 specimen collected (MECN 5772).

Localities. Sabayan (14).

Literature records. Portovelo (Anthony 1921).

Identification. Dorsal fur bright grayish brown. Venter coat white to yellowish gray. Eyes small, ears small but

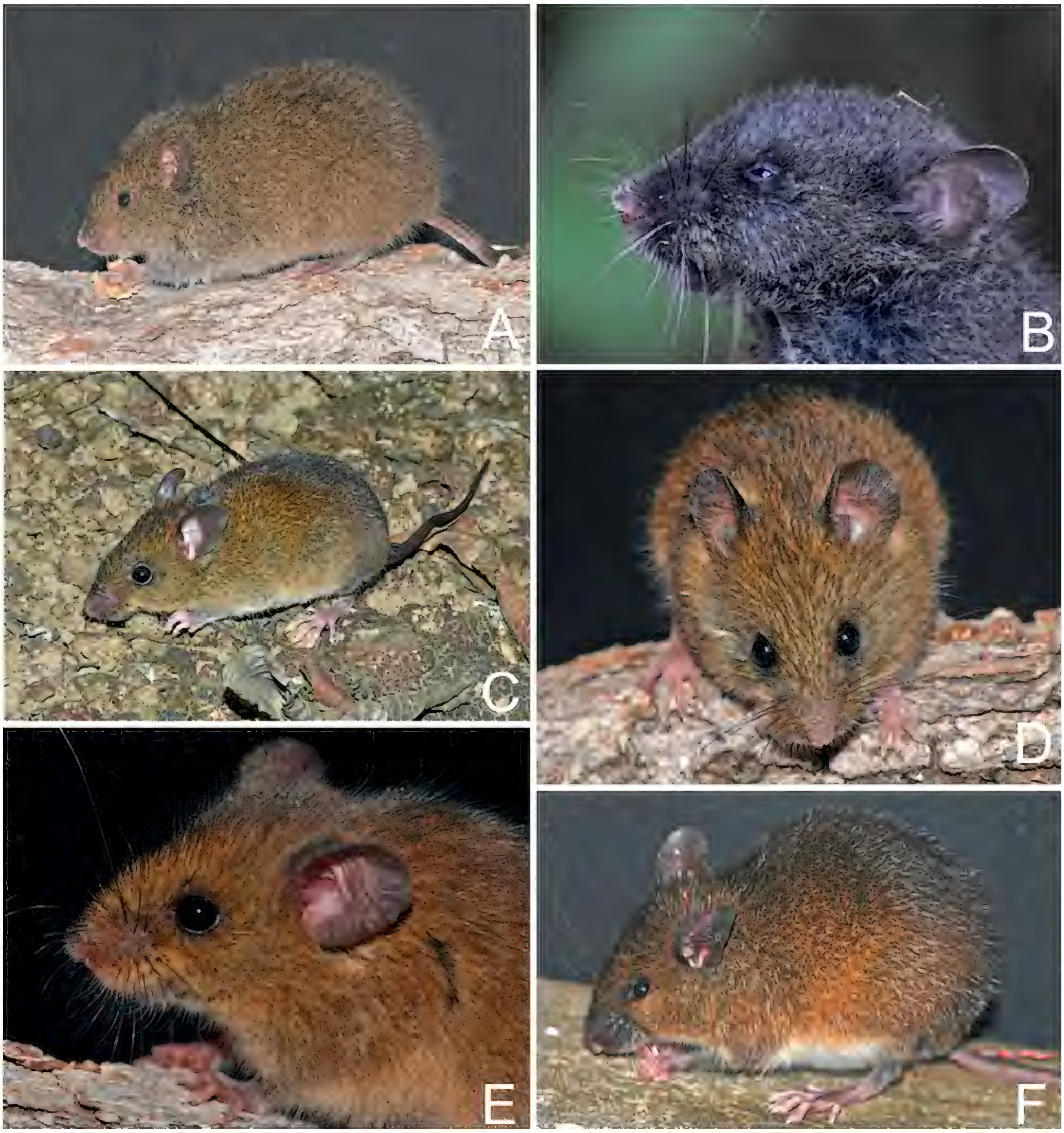

Fig. 7. Some cricetid rodents of the Provincia de El Oro. **A**. *Akodon mollis* (MECN 4727) recorded in the Sabadel. **B**. *Chilomys neisi* (MECN 6187) recorded in the Ashigsho. **C**. "*Handleyomys*" *alfaroi* (MECN 5762) recorded in the El Guayabo. **D**. *Microryzomys altissimus* (MECN 4708) recorded in the Laguna de Chinchilla. **E**. *Microryzomys minutus* (MECN 4810) recorded in the Chillacocha. **F**. *Nephelomys albigularis* (4834) recorded in the Payana (Photos by J. Brito).

visible on the coat (Fig. 8). Supraorbital vibrissa absent. Tail uniformly dark, shorter than the length of the head and body together, covered with fine hairs that hide the scales. Hindfoot long, paddle or wedge-shaped, with a narrow heel and broad sole. Soles blackish. Outer edges of feet and toes have a fringe of stiff, silver to white hairs that curve downward. Digits have small interdigital webs near bases. Cranially, rostrum broad, cranium massive with widened zygomatic arches. Lower third molars bilobed (Voss 2015).

Ecological notes. The only individual was captured on the banks of a small canyon stream. For two days it was kept in captivity and fed with small fish (sardines), which were quickly devoured starting with the head of the fish (Fig. 8).

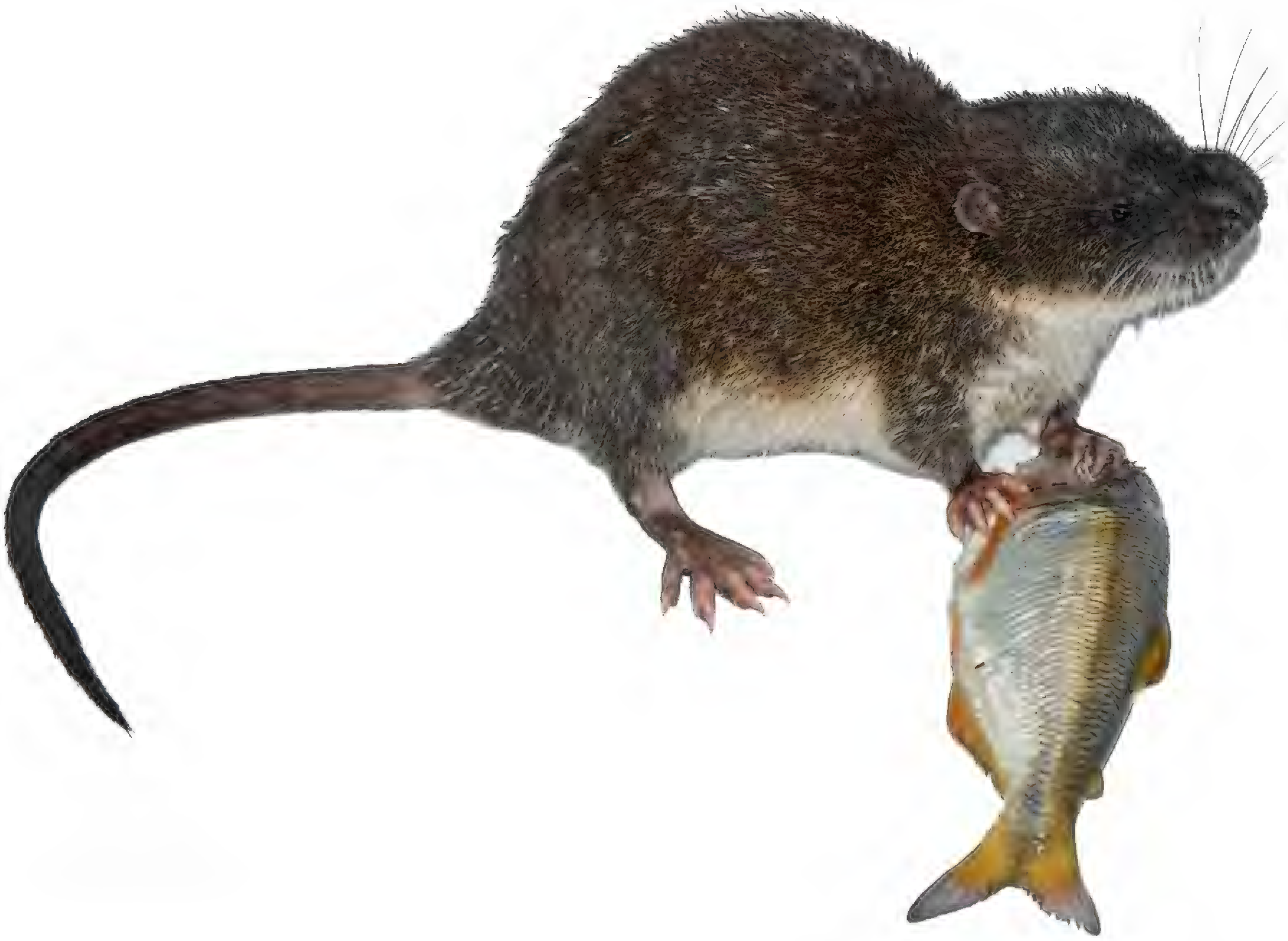

Fig. 8. Tweedy's Crab-eating Rat, *Ichthyomys tweedii* (MECN 5772), recorded in the Sabayan, Provincia de El Oro (Photo by J. Brito).

Conservation status. National, Endangered (EN); Global, Data Deficient (DD).

Ecological notes. A male with scrotal testes measuring 12 x 9 mm was recorded in November 2018.

Remarks. With type locality in Ecuador: "Portovelo, Prov. del Oro, Ecuador; altitude, 2000 ft." (Anthony 1921:1).

Melanomys caliginosus (Tomes, 1860)

Material. None.

Literature records. Santa Rosa (Weksler & Lòss 2015).

Identification. Robust, small, head-body length 95–117 mm. Dorsal fur dark brown, with tips of hairs orange. Dorsal surface of legs and hands black and covered with dark hairs. Tail short (91–92% of the head-body length). Skull with short incisive foramina, hourglass-shaped interorbital region, and presence of ridges.

Conservation status. National, Near Threatened (NT); Global, Least Concern (LC).

Remarks. With type locality in Ecuador: "Ecuador" (stated by J. A. Allen [1913:537] to be "doubtless Esmeraldas [Esmeraldas] (near sea level), Ecuador").

Microryzomys altissimus (Osgood, 1933)

Material. 4 specimens collected (MECN 4704, 4708, 4828, 4719).

Localities. Payana (44), Cerro de Arcos 835), Laguna de Chinchilla (36).

Identification. Small, head-body length 70–73 mm. Dorsal coat olive-brown; belly yellowish gray (Fig. 7D). Tail long, greater than 110 mm and longer than the total length of the head and body combined, noticeably bicolored, dark above. Skull with long, wide incisive foramina. Dentary with small incisor tubercle (Carleton & Musser 1989).

Conservation status. National and Global, Least Concern (LC).

Microryzomys minutus (Tomes, 1860)

Material. 2 specimens collected (MECN 4700, 4810).

Localities. Laguna de Chinchilla (36), Chillacocha (45).

Literature records. Tarahuacocha and El Chiral (Carleton & Musser 1989).

Other specimens. MEPN 5842, 5864.

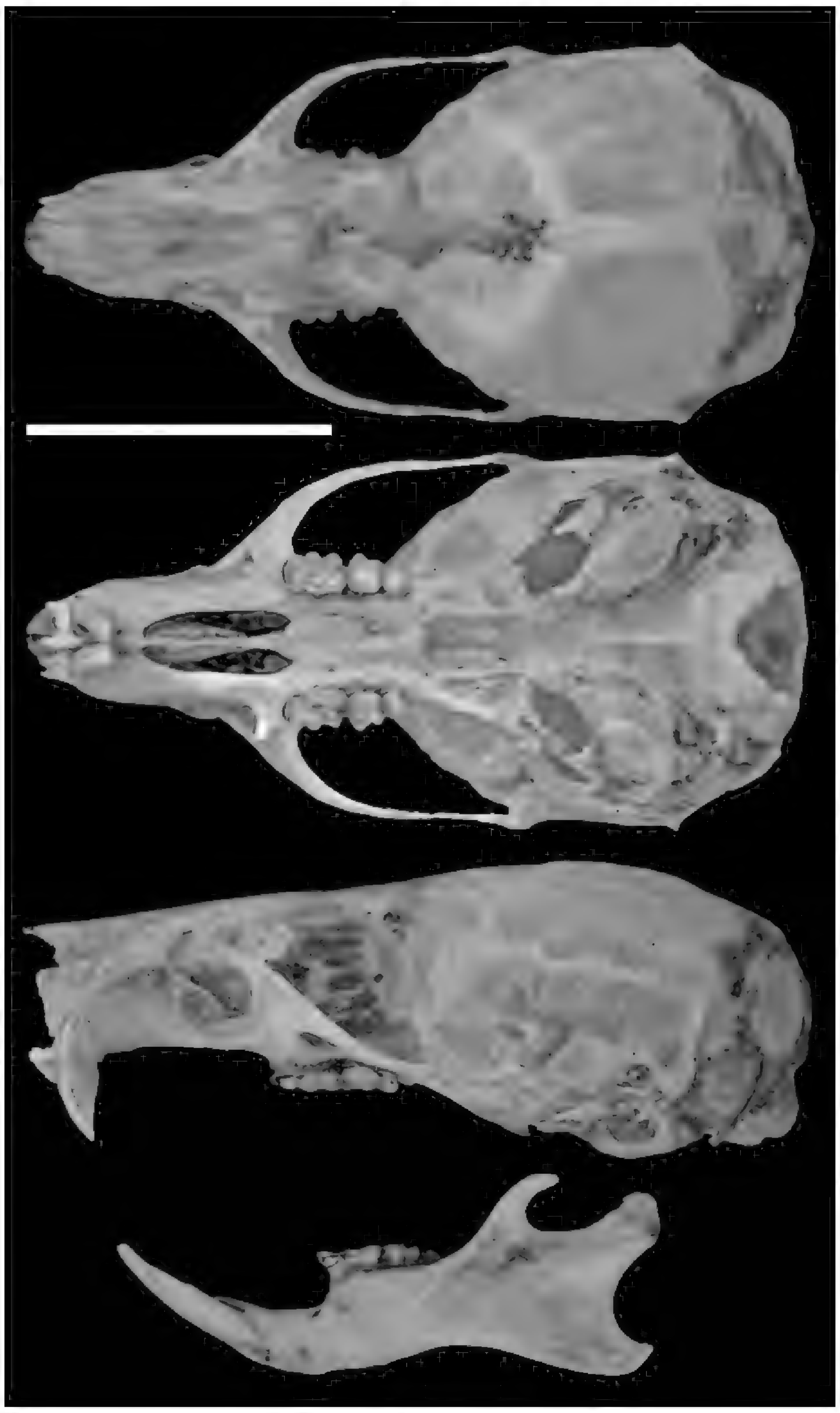

Fig. 9. Dorsal, ventral, and lateral view of the skull of *Neusticomys orcesi* (MECN 6185) recorded in the Cabecera del Rio Casacay, Provincia de El Oro. Scale 10 mm (Photos by J. Brito).

Identification. Small, head-body length 65–80 mm. Dorsal coat yellowish brown and belly yellow or pale orange (Fig. 7E). Tail long (161% of the head-body length), and dark. Hind legs with protruding pads. Skull with long and wide incisive foramina. Dentary with distinct incisor tubercle (Carleton & Musser 1989).

Conservation status. National and Global, Least Concern (LC).

Remarks. With type locality in Ecuador: probably near Pallatanga, on the western slope of the Cordillera, Chimborazo, Ecuador (see Carleton & Musser 1989:65).

Nephelomys albigularis (Tomes, 1860)

Material. 52 specimens collected (MECN 4784–4788, 4798, 4799, 4803, 4804, 4813, 4823–4825, 4833, 4834, 4888, 4892, 4903, 4913, 6825, 6828, 6936, 6937, 6940, 6943, 6946, 6949, 6950, 6970–6974, 6976, 6977, 6979, 6985, 6988, 6989, 6991, 6992, 6995, 6997, 6998–7006, 7010, 7011, 7017).

Localities. Ashigsho, Rancho Triste (41), Cabecera del Rio Casacay (39), Chillacocha (45), Chivaturco (31), Ashigsho, vía Gallo Cantana (40), Payana (44), Yacuviñay (29), Güishiguiña (29).

Literature records. El Chiral and Salvias (Weksler 2006).

Other specimens. MEPN 6045, 6046, 6098.

Identification. Dorsal coat ranges from grayish orange (in adults, Fig. 7F) to dark brown (in juveniles). Ventral coat whitish to yellowish (in adults) to grayish (in juveniles). Tail bicolor or weakly bicolor (few specimens with unicolor tail). Most specimens with small white spot in the gular region, and in only three specimens does this spot extend to the pectoral region. Skull with short incisive foramina (Percequillo 2015a). Alisphenoid strut usually absent, thin when present.

Ecological notes. Between November and December 2015, nine males with scrotal testicles and one pregnant female were recorded.

Conservation status. National, Vulnerable (VU); Global, Least Concern (LC).

Remarks. With type locality in Ecuador: "Taken *en camino* on my return from Pallatanga"; Provincia de Chimborazo, Ecuador (Tomes 1860: 264).

Neusticomys orcesi (Jenkins & Barnett, 1997)

Material. 2 specimens collected (MECN 6185, 6186).

Locality. Cabecera del Río Casacay (39).

Identification. Dorsal fur dull grayblack brownish, ventral pelage slightly paler than dorsum. Pinnae conspicuous above fur on head. Philtrum present. Tail slightly shorter than head-and-body length, with abundant hair. Hind feet with a row of stiff hairs on the edge of the metatarsus and digits. Rostrum slender; inferior root zygomatic plate posterior to the first upper molar; petrosal well exposed; occipital condyles not projecting posteriorly beyond rest of occiput (Fig. 9).

Ecological notes. Two individuals were captured on the banks of a small mountain stream (Fig. 10B–C). They were kept in captivity for two days and fed with aquatic invertebrate larvae. The habitat was thickly vegetated with zurales (*Chusquea* sp.), and emergent trees such as *Cedrela* sp., and *Ficus* sp.

Taxonomic notes: This species was described within *Chibchanomys* (Jenkins & Barnett 1997; Voss 2015); very recently Salazar-Bravo et al. (2023), based on molecular and morphological evidence, transfer it to *Neusticomys*. Voss (2015) reports a record in Perú based on the specimen LSUMZ 14406 (Museum of Zoology of Louisiana State University, Baton Rouge). However, in the extensive revision of Salazar-Bravo et al. (2023), this animal is regarded as an undescribed species of *Chibchanomys*. Therefore, our specimens of *N. orcesi* collected in

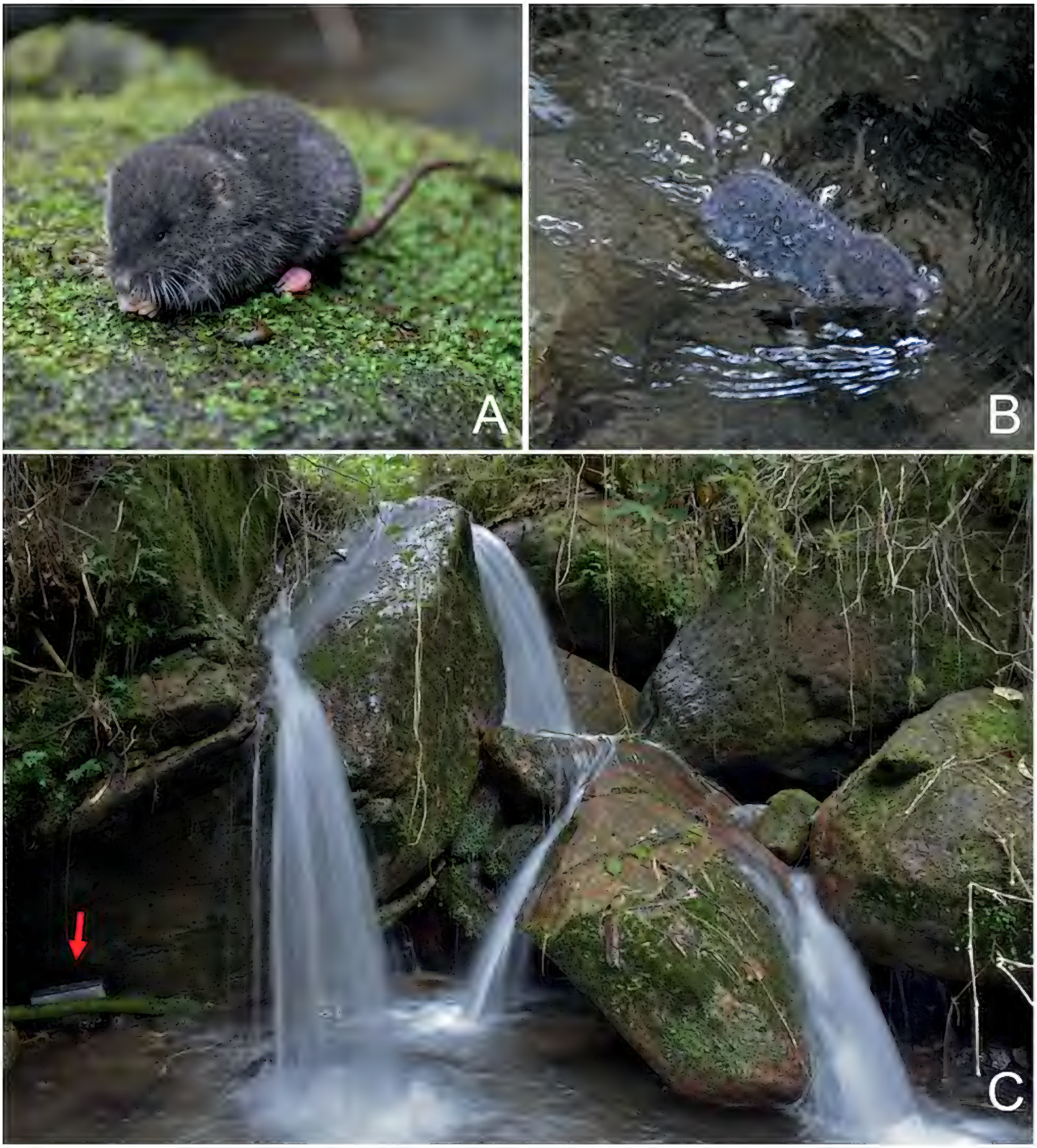

Fig. 10. Orcés' Water Mouse. **A–B**. *Neusticomys orcesi* (MECN 6185), external appearance. **C**. Capture site in the Cabecera del Rio Casacay, note the location of the trap, pointed by an arrow (Photos by J. Brito).

the Río Casacay correspond to the second locality for this species. In addition, it represents the lowest altitude record (2,000 m. a.s.l.). Previously the species was known only from around the Lake Luspa type locality in Cajas National Park (Ecuador), above 3,100 m. a.s.l. (Jenkins and Barnett 1997).

Conservation status. National, Critically Endangered (CR); Global, Data Deficient (DD).

Remarks. Species endemic to Ecuador, type Locality. Lake Luspa, Parque Nacional Cajas, Provincia Azuay, Ecuador, 02°50′ S 79°30′ W, altitude 3700 m (Jenkins & Barnett 1997: 124).

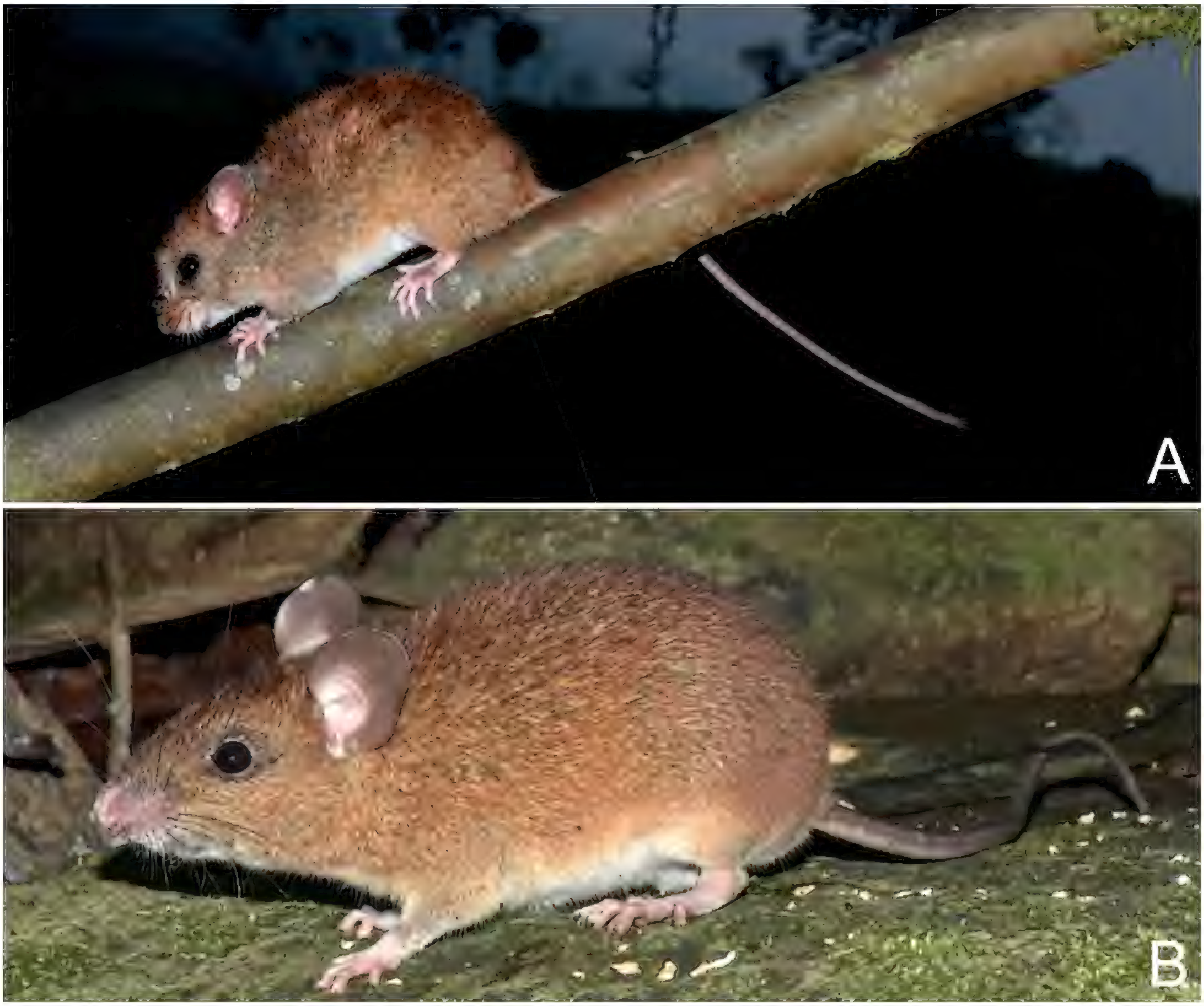

Fig. 11. A. *Oecomys bicolor* (MECN 5757) recorded in the El Guayabo. **B**. *Transandinomys talamancae* (MECN 6148) recorded in the Puyango, Provincia de El Oro (Photos by J. Brito).

Oecomys bicolor (Tomes, 1860)

Material. 1 specimen collected (MECN 5757).

Locality. El Guayabo (13).

Identification. Small, head-body length 107 mm. Hair smooth and long (9 mm). Back orange, with gray base. Belly white, contrasting with back (Fig. 11A). Tail not so long (125 mm) in comparison to head-body length (116%), and with a small 6 mm brush at its tip. Skull with short rostrum, narrow interorbital with finely beaded supraorbital ledges (Fig. 12). Temporal ridges weakly defined. Zygomatic plates narrow and dorsal notches shallow. Incisive foramina relatively short and wide, their posterior margins do not reach the anterior margin of the first molars. Alisphenoid strut present, and wide. Ectotympanic bulla small, exposing much of the medial periotic. Dentary with small incisor tubercle.

Taxonomic notes: Our specimen corresponds to the first record of the genus in southwestern Ecuador. It is known that *Oecomys bicolor* represents a complex of species (Carleton & Musser 2015). Within the complex, the trans-Andean forms, such as *O. dryas*, deserve special attention. We agree with Carleton & Musser (2015) and conceive that a systematic revision of *Oecomys* in western Ecuador, including genetic and morphological evidence, is needed.

Conservation status. National and Global, Least Concern (LC).

Remarks. With type locality in Ecuador: Gualaquiza, Río Gualaquiza, 885 m, Morona Santiago, Ecuador (Tomes 1860).

Oligoryzomys destructor (Tschudi, 1844)

Material. None.

Literature records. Piñas (Weksler & Bombicino 2015).

Identification. Dorsal fur reddish brown, while belly yellowish white. Dorsal surfaces of feet covered by short

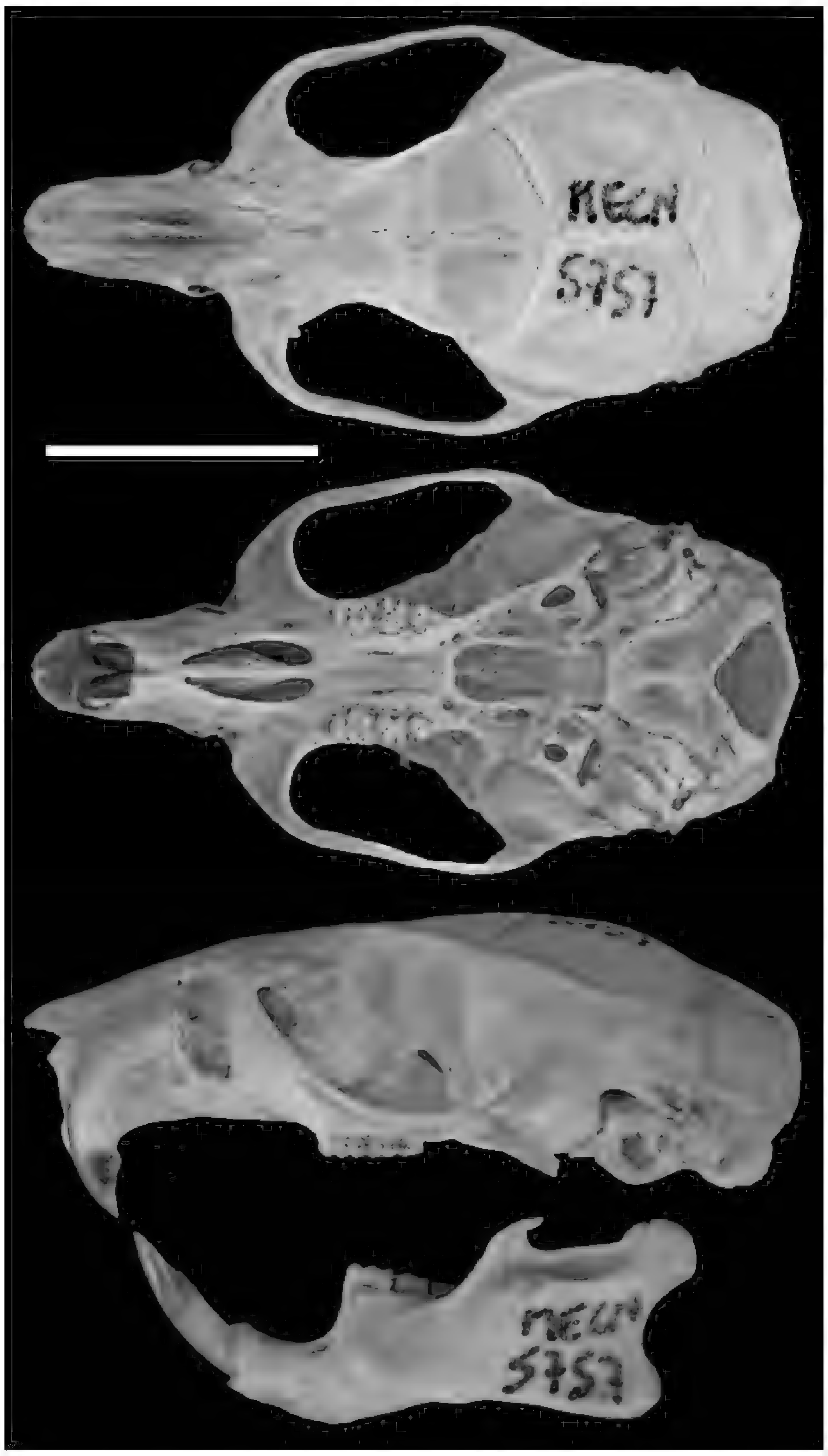

Fig. 12. Dorsal, ventral, and lateral view of the skull of *Oecomys bicolor* (MECN 5757) recorded in the El Guayabo, Provincia de El Oro. Scale 10 mm (Photos by J. Brito).

silver-gray hair, with hairs of nail base very long. Tail brown and slightly shorter than the head and body length; vibrissae black on basal half and white toward tip; nose hair silver white (Weksler & Bombicino 2015).

Conservation status. National: National and Global, Least Concern (LC).

Oreoryzomys balneator (Thomas, 1900)

Material. 1 specimen collected (MECN 4789).

Localities. Chivaturco (31).

Literature records. El Chiral (Anthony 1924b; Weksler 2006).

Identification. Small body size, with head and body length (85 mm); tail longer than head and body (113 mm); hindfeet narrow (25 mm); ears long and rounded (17 mm). Dorsal pelage short, whit hairs 6 mm in length, darkly colored (Fig. 13A); ventral pelage is even shorter (5 mm), grayish. Throat with small white patch. Tail uniformly dark brown. Skull small (20.3 mm incisive condyle length). Superficial zygomatic notch. Very small lacrimals. Frontal parietal suture “U” shaped. Posterior border of zygomatic plate aligned with the procingulum of first upper molar (Fig. 14).

Taxonomic notes: Anthony (1924b) described *Oreoryzomys balneator hesperus* based on a specimen collected in El Chiral, Provincia de El Oro. Our specimen is morphologically like *O. b. hesperus*. In an in progress revision of *O. balneator* from several localities in Ecuador, it has been detected that it may be a complex of at least three different species (Brito, pers. obs.).

Conservation status. National, Near Threatened (NT); Global, Data Deficient (DD).

Remarks. With type locality in Ecuador: Mirador, Baños, Tungurahua, Ecuador (Thomas 1900).

Phyllotis andium Thomas, 1912

Material. None.

Literature records. Taraguacocha (Rengifo & Pacheco 2015).

Identification. Dorsal fur brown with tips of some bright reddish-brown hairs giving it a marbled appearance. Ventral fur pale gray. Relatively large ears. Tail covered with light hairs and longer than the length of the head and body.

Conservation status. National: National and Global, Least Concern (LC).

Remarks. With type locality in Ecuador: Cañar, Provincia de Cañar, Ecuador. Alt. 2600 m (Thomas 1912).

Phyllotis sp.

Material. None.

Literature records. Jambelí (Orihuela-Torres et al. 2019).

Remarks. *Phyllotis* sp. was recovered from the pellets of the Northern Caracara *Caracara cheriway*, in the locality of Jambelí at 5 m (Orihuela-Torres et al. 2019). Currently, no species of *Phyllotis* has been reported from the Ecuadorian coast. However, there are some *Phyllotis* that can inhabit the coast, such as *P. amicus* and *P. gerbillus* in northern Peru and the border with Ecuador (Rengifo & Pacheco 2015). The collection of additional material in Jambelí is necessary to corroborate the status of this form.

Rhipidomys latimanus (Tomes, 1860)

Material. None.

Literature records. El Retiro (Brito et al. 2018).

Identification. Dorsal coat orange to reddish brown. Ventral fur creamy white. Tail longer than the head and body combined, dark brown, with a distinctive brush-like tuft of hairs distally. Eyes large.

Conservation status. National and Global, Least Concern (LC).

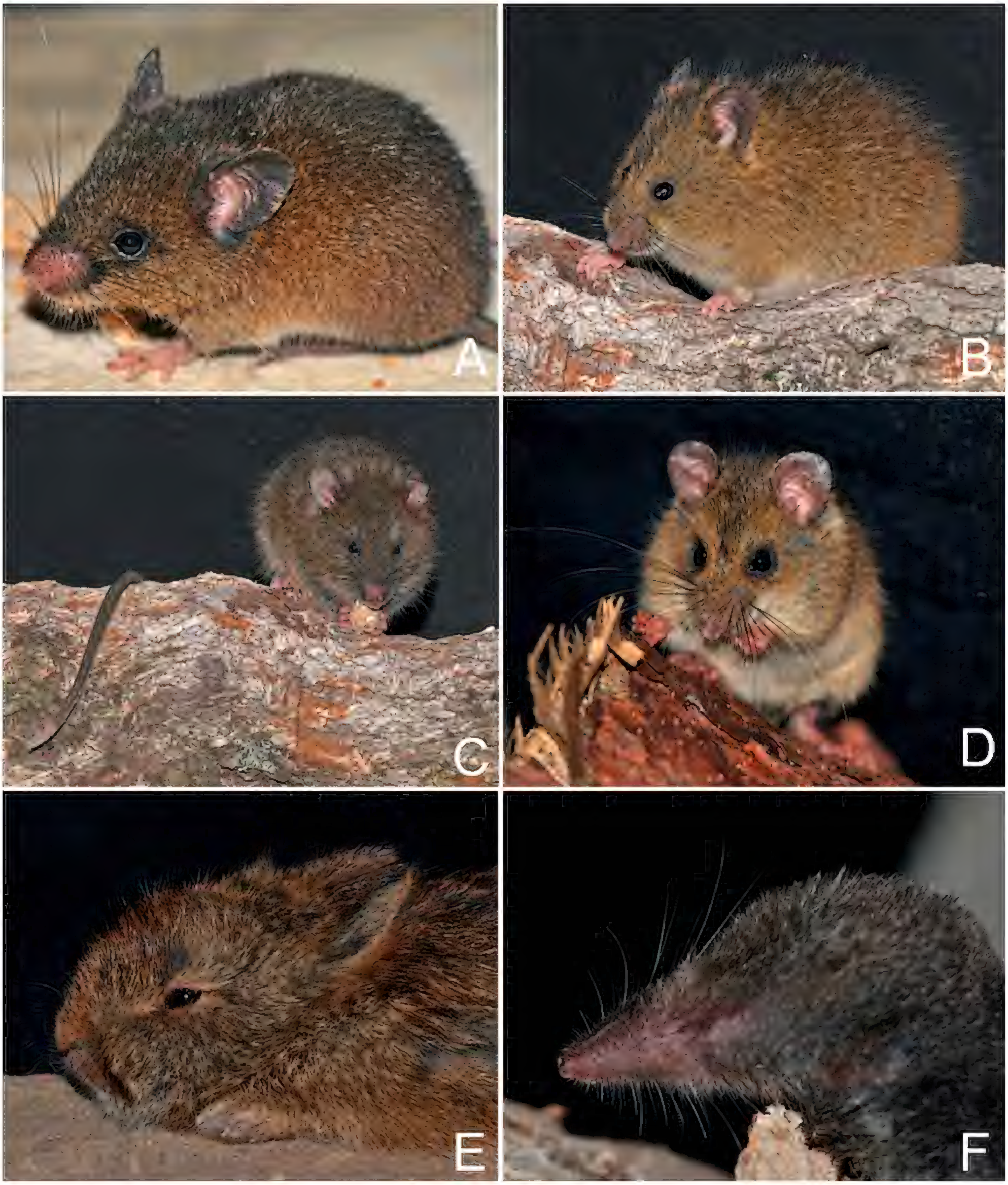

Fig. 13. Some small mammals of the Provincia de El Oro. **A**. *Oreoryzomys balneator* (MECN 4789) recorded in the Chivaturco. **B**. *Thomasomys auricularis* (MECN 4686) recorded in the Cerro de Arcos. **C**. *Thomasomys caudivarius* (MECN 4729) recorded in the Sabadel. **D**. *Thomasomys taczanowskii* (4822) recorded in the Chillacocha. **E**. *Sylvilagus andinus* (MECN 4685) recorded in the Cerro de Arcos. **F**. *Cryptotis montivagus* (MECN 4716) recorded in the Laguna de Chinchilla (Photos by J. Brito).

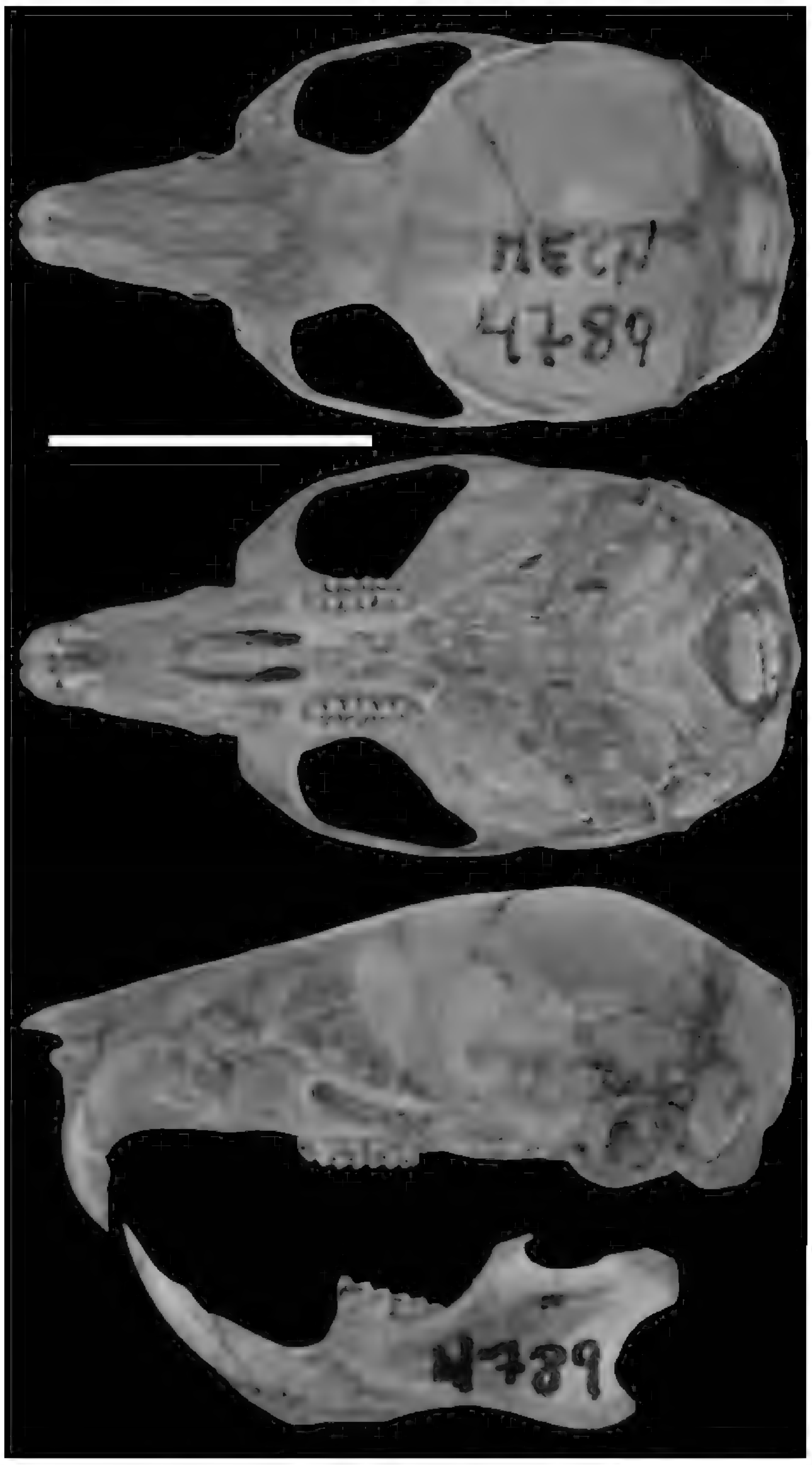

Fig. 14. Dorsal, ventral, and lateral view of the skull of *Oreoryzomys balneator* (MECN 4789) recorded in the Chivaturco, Provincia de El Oro. Scale 10 mm (Photos by J. Brito).

Remarks. With type locality in Ecuador: around Pallatanga, Provincia de Chimborazo, Ecuador (Tomes 1860).

Rhipidomys leucodactylus (Tschudi, 1845)

Material. None.

Literature records. Los Pozos (Tribe 2015).

Identification. Largest species within the genus (Tribe 2015). Dorsal coat brown, with yellowish tones, and with dark guard hairs. Venter coat woolly yellowish. Tail uniform reddish to dark brown, with a long tuft of hairs distally. Skull large and robust, with well-developed supraorbital ridges.

Conservation status. National and Global, Least Concern (LC).

Sigmodon peruanus J. A. Allen, 1897

Material. 1 specimen collected (MECN 6383).

Locality. Reserva Ecológica Arenillas (9).

Literature records. Piedras, Portovelo, and Santa Rosa (Voss 1992).

Identification. Dorsal fur grayish clay brown with intermingled black hairs and a few protruding hairs with white tips. Ventral coat grayish brown, with the base of the hairs dark gray. Dorsum of hind foot covered with grayish brown hairs. Tail shorter than the length of the head and body combined. Tail bicolor, dark above and

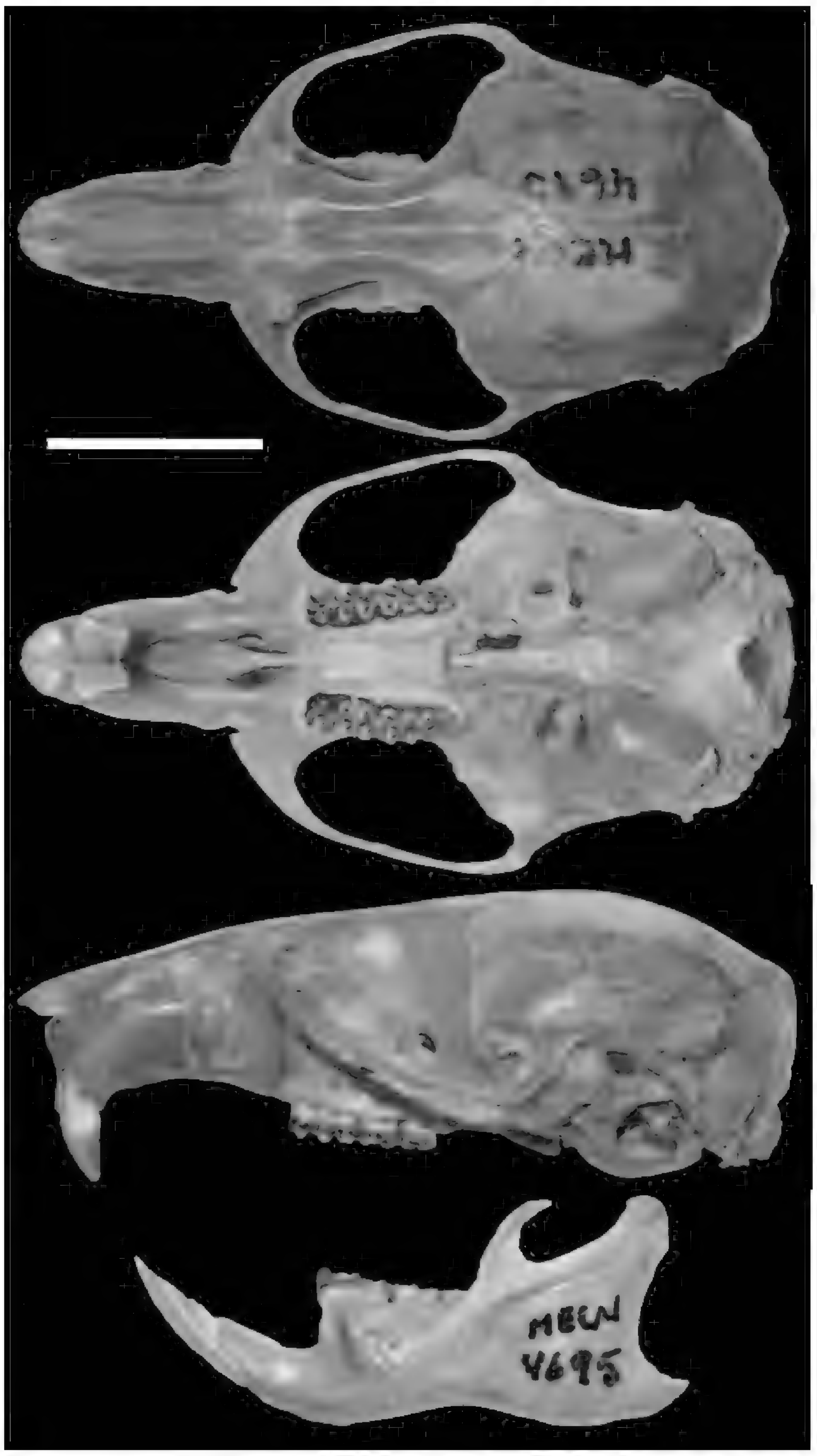

Fig. 15. Dorsal, ventral, and lateral view of the skull of *Thomasomys auricularis* (MECN 4686) recorded in the Cerro de Arcos, Provincia de El Oro. Scale 10 mm (Photos by J. Brito).

pale below. Molars lacking mesoloph or mesolophid, flat crowned, with principal cusps and crests connected in a more or less continuous sigmoidal pattern.

Conservation status. National, Near Threatened (NT); Global, Least Concern (LC).

Remarks. The only specimen recorded, represented by both dentaries, was retrieved from the stomach contents of *Leopardus garleppi* (MECN 6170).

Thomasomys auricularis Anthony, 1923

Material. 2 specimens collected (MECN 4686, 4695).

Locality. Cerro de Arcos (35).

Literature records. Tarahuacocha (Anthony, 1923).

Identification. Dorsal coat tawny olive, interspersed with blackish hairs (Fig. 13B). Ventral coat yellowish, more intense on the pectoral area. Post auricular patch of ochraceous color. Tail relatively long (122–134% of the head-body length), covered with small hairs. Incisive foramina long extending to the procingulum of the first upper molar. Auditory bulla large and inflated (Fig. 15).

Ecological notes. Two males with scrotal testicles we recorded in September 2015.

Conservation status. National, Vulnerable (VU); Global, Data Deficient (DD).

Remarks. Species endemic to Ecuador, type Locality. "Taraguacocha, on trail from Zaruma to Zaraguro, altitude 10,250 feet, Cordillera de Chilla, Provincia del Oro, Ecuador." (Anthony 1923:6).

Thomasomys baeops (Thomas, 1899)

Material. None.

Previous records: Taraguacocha (Pacheco 2015).

Identification. Dorsal fur dull grayish brown, darker towards the midline of the back. Ventral coat silvery gray color. Tail longer than the body and head combined. Rostrum short; nasals short and narrow; braincase moderately inflated, and interorbital region narrow. Incisive foramina narrow with contracted ends and moderately long, reaching the upper first molars. Auditory bulla small and not inflated.

Conservation status. National and Global, Least Concern (LC).

Remarks. With type locality in Ecuador: Río Pita, above the Valle de los Chillos, Provincia de Pichincha, Ecuador. Alt. 3,500 m (Thomas 1899).

Thomasomys caudivarius Anthony, 1923

Material. 18 specimens collected (MECN 4687, 4689, 4690–4692, 4697, 4702, 4703, 4705, 4709, 4714, 4715, 4728, 4729, 4809, 4818, 7022).

Localities. Ashigsho, Rancho Triste (41), Cerro de Arcos (35), Chillacocha (45), Laguna de Chinchilla (36), Sabadel (34).

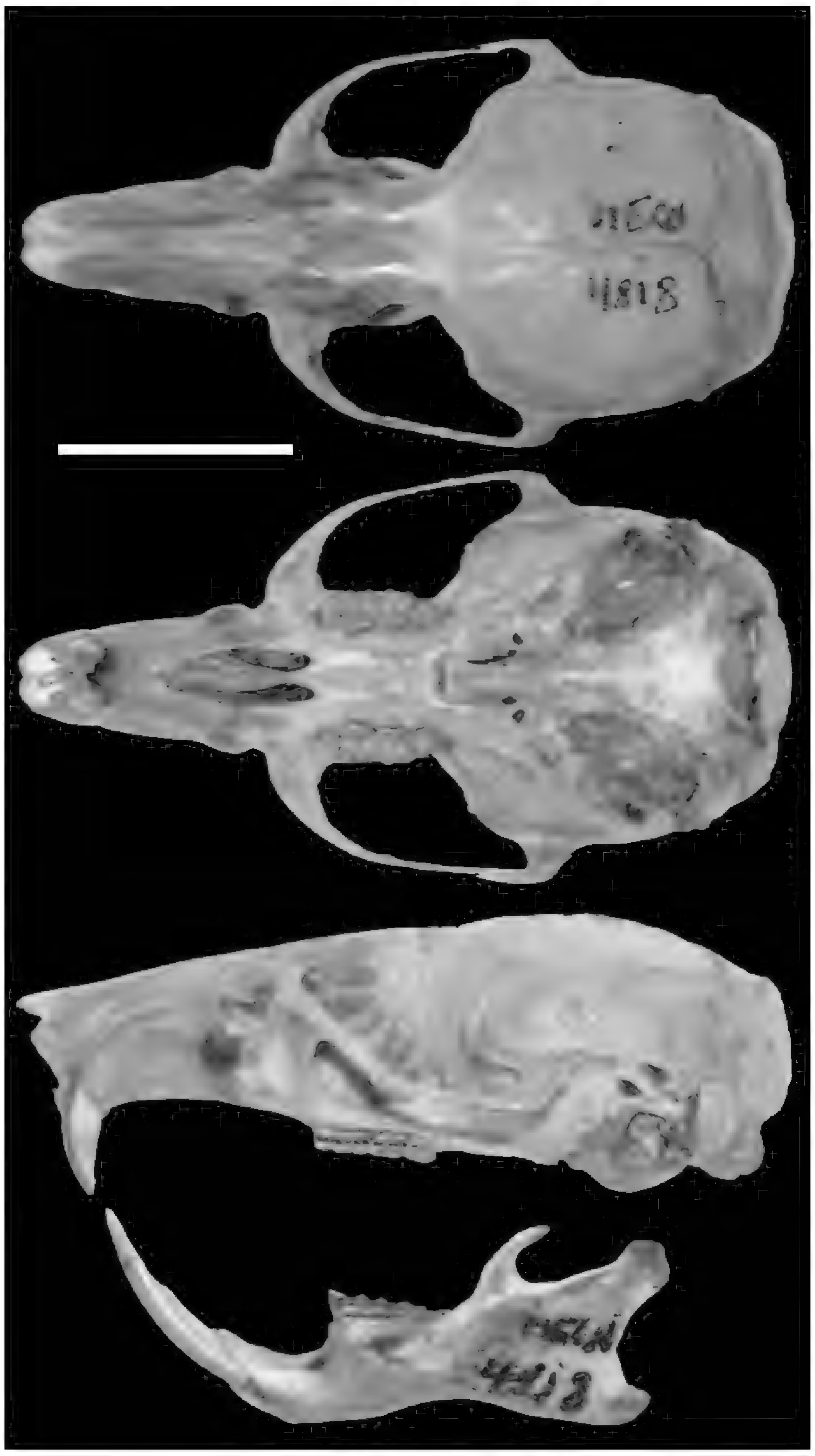

Fig. 16. Dorsal, ventral and lateral view of the skull of *Thomasomys caudivarius* (MECN 4818) recorded in the Chillacocha, Provincia de El Oro. Scale 10 mm (Photos by J. Brito).

Literature records. Taraguacocha (Anthony 1923).

Identification. Dorsal coat with gray base and yellow apex (Fig. 13C). Ventral fur with gray base and pale orange apex. Tail uniformly dark (132.4% of the head-body length) and with tip (10–45 mm) generally white. Shallow zygomatic notch (Fig. 16).

Ecological notes. Three males with scrotal testes were recorded in September 2015.

Conservation status. National, Vulnerable (VU); Global, Least Concern (LC).

Remarks. With type locality in Ecuador: "Taraguacocha, Cordillera de Chilla, 10,750 feet [3,277 m], Provincia del Oro, Ecuador" (Anthony 1923: 4).

Thomasomys taczanowskii (Thomas, 1882)

Material. 34 specimens collected (MECN 4698, 4701, 4731, 4781, 4791, 4805, 4814, 4815, 4816, 4822, 4836, 4842, 4844, 4846, 4893, 4895, 4910, 4912, 6827, 6932, 6935, 6236, 6939, 6941, 6942, 6969, 6978, 6981, 6982, 6986, 6987, 6993, 7020, 7023).

Localities. Yacuviñay (28), Chivaturco (31), Sabadel (34), Cerro de Arcos (35), Laguna de Chinchilla (36), Cabecera del Rio Casacay (39), Ashigsho, vía Gallo Cantana (40), Ashigsho, Rancho Triste (41), Ashigsho, El Tanque (42), Shiñinguro (43), Payana (44), Chillacocha (45),

Literature records. Cordillera de Chilla (Pacheco 2015).

Identification. Dorsum fur grayish with reddish yellow hair tips (Fig. 13D). Ventral coat grayish white. Tail uniformly pale brown. Legs white, with a brownish appearance on the metacarpals and metatarsals. Skull with moderately broad orbital region. Inflated auditory bulla. Zygomatic arches converge anteriorly. Incisive foramina long and narrow, extending slightly between the anterocones of the first upper molars.

Conservation status. National, Not Evaluated (NT); Global, Least Concern (LC).

Transandinomys talamancae (J. A. Allen, 1891)

Material. 15 specimens collected (MECN 4864, 4866–4868, 5750, 5751, 5768, 5769, 5770, 5771, 6035, 6037–6039, 6148).

Localities. Puyango (12), Sabayan (14).

Identification. Dorsal fur short (8–10 mm) and thick, orange-brown (Fig. 11B). Ventral coat whitish but with gray base. Tail slender and bicolored, dark above and whitish below. Tail equal to or slightly longer (119–325 mm) than the length of the head-body (120–132 mm), bare in appearance but finely covered with small hairs. Cranium has narrow interorbitals and poorly developed supraorbital ridges, short incisive foramina. Zygomatic plate wide and excavated. Deep zygomatic notch.

Ecological notes. In December 2016, four adult males were recorded with scrotal testicles (average 8 x 4 mm), plus one lactating female.

Conservation status. National and Global, Least Concern (LC).

Family Echimyidae Gray, 1825

Proechimys decumanus (Thomas, 1899)

Material. 1 specimen collected (MECN 5521).

Localities. Reserva Ecologica Arenillas (9).

Literature records. Santa Rosa (Patton & Leite 2015).

Other Material. MEPN 9965–9968.

Identification. Dorsal color sandy fawn with darker hairs intermingled. Tail bicolor, dark above and pale below, covered with short fine hairs. Temporal ridges moderately developed and continuous across parietals from posterior end of supraorbital flange.

Conservation status. National and Global, Near Threatened (NT).

Remarks. With type locality in Ecuador: Chongón, Provincia de Guayas, west of Guayaquil, Ecuador (Thomas 1899).

Proechimys semispinosus (Tomes, 1860)

Material. 1 specimen collected (MECN 6150).

Locality. El Guayabo (13), Sabayan (14).

Literature records. Santa Rosa (Thomas 1900).

Identification. Length of head and body 276 mm and the length of the tail (205 mm). Length of hind legs 65 mm; length of ears 25 mm; weight 450 g. Dorsal color dark reddish brown (Fig. 17), splashed with black, and sides only slightly paler to contrast with uniformly white belly. Tail dark brown above and pale below. Tail lined with sparse, elongated hairs. Dorsal coat stiff to the touch. Spines long (21 mm), wide (0.9). Each aristiform ends in an elongated and filamentous tip. Skull large (greatest skull length 65.8 mm). Species uniquely characterized among spiny rats by their well-developed temporal ridges extending from supraorbital ledge across length of parietals.

Conservation status. National, Near Threatened (NT); Global, Least Concern (LC).

Remarks. With type locality in Ecuador: Esmeraldas, Provincia de Esmeraldas, on the Pacific coast of Ecuador (Tomes 1860).

Family Muridae Illiger, 1811

Mus musculus Linnaeus, 1758

Material. 1 specimen collected (MECN 4832).

Localities. Payana (44).

Literature records. Las Casitas, Jambelí (Orihuela-Torres et al. 2018, 2019).

Remarks. Invasive alien species.

Rattus rattus Linnaeus, 1758

Material. 3 specimens collected (MECN 6145, 5761, 4840).

Localities. El Guayabo (13), Sabayan (14), Payana (44).

Literature records. Las Casitas and Las Huacas-Jambelí (Orihuela-Torres et al. 2018, 2019).

Remarks. Invasive alien species.

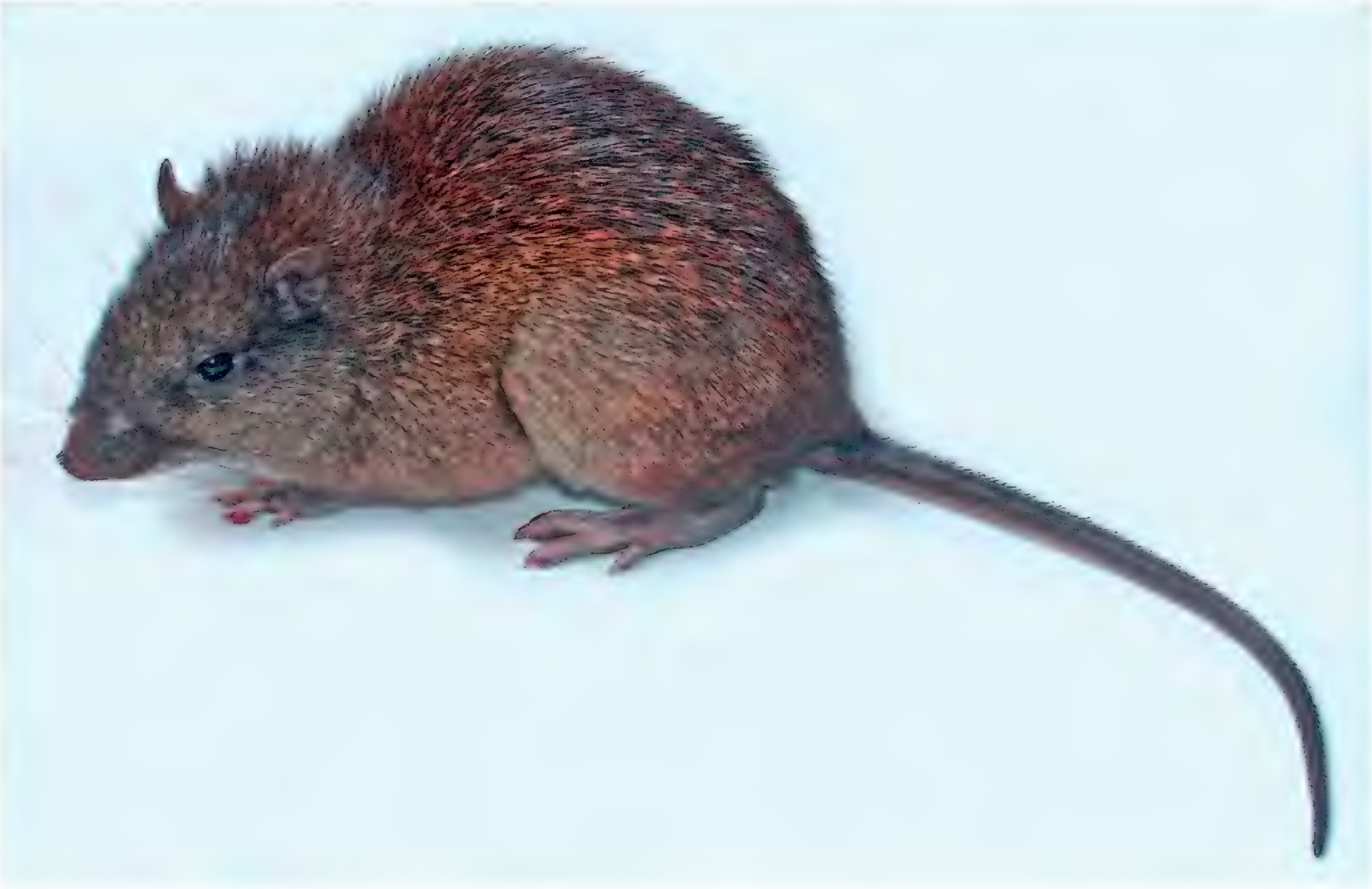

Fig. 17. Tome's Spiny Rat, *Proechimys semispinosus* (MECN 6150) recorded in the Sabayan, Provincia de El Oro (Photo by R. García).

Order Lagomorpha Brandt, 1855

Family Leporidae Fischer, 1817

Sylvilagus andinus (Thomas, 1897)

Material. 1 specimen collected (MECN 4685).

Localities. San Patricio (22), Yacuviñay (28), Chivaturco (31), Cerro de Arcos (35), Laguna de Chinchilla (36), Ashigsho, Rancho Triste (42), Shiñinguro (43), Payana (44), Chillacocha (45).

Literature records. Portovelo, Taraguacocha, and Vía Salvias Zaruma (Anthony 1923).

Identification. Coat blackish (Fig. 13E), mottled with black and fawn. Chin and ventral region of opaque whitish color. Ears short and rounded with grayish base, blackish brown towards the middle of its length. Cranium without dimples on the dorsal surface; postorbital process small (Ruedas et al. 2019).

Conservation status. National, Near Threatened (NT); Global, Data Deficient (DD).

Remarks. With type locality in Ecuador: W. slope of Cayambe Mountain, Provincia de Pichincha, Cantón Cayambe, Eastern Cordillera of Ecuador, altitude 4,000 m (Thomas 1897).

Sylvilagus daulensis Allen, Richardson, and Chapman 1914

Material. None.

Museum specimens: Reserva Ecológica Arenillas (Ruedas et al. 2019).

Identification. Similar in coloration to the *Sylvilagus andinus*, but with more accentuated and colorful shades. Posteromedial aspect of petrosal extends between the bulla and the basioccipital almost to alisphenoid. *S. daulensis* is the only rabbit species inhabiting the southwestern coast of Ecuador (Ruedas et al. 2019).

Conservation status. National, Near Threatened (NT); Global, Not Evaluated.

Remarks. Species endemic to Ecuador, type Locality. Daule, Provincia de Guayas, Ecuador (Allen et al. 1914).

Order Eulipotyphla Waddell, Okada, & Hasegawa, 199

Family Soricidae Fischer, 1817

Cryptotis montivagus (Anthony, 1921)

Material. 3 specimens collected (MECN 4711, 4713, 4716).

Locality. Laguna de Chinchilla (36).

Identification. Small, 78–88 mm head-body length. Back dark gray, ventral region paler than the back and silvery in appearance. Head long and pointed. Ears very short and often imperceptible among the fur. Eyes extremely small (Fig. 13F).

Conservation status. National, Near Threatened (NT); Global, Least Concern (LC).

Remarks. Species endemic to Ecuador, type Locality. "Bestion, Prov. del Azuay, Ecuador; altitude 10,000 ft" (Anthony 1921:5).

Order Carnivora Bowdich, 1821
Family Mustelidae G. Fischer, 1817

Galictis vittata (Schreber, 1776)

Material. None.

Locality. Reserva Ecologica Arenillas (García-Olaechea et al. 2021), Reserva Buenaventura (Brito et al. 2018).

Identification. Head small and flattened, ears wide, rounded and whitish. Small eyes. Top of the head, back, sides and tail gray. Face, throat, belly and legs black (Fig. 18A). Diagonal band of white or cream color runs from forehead to shoulders separated by a dorsal gray and ventral black color (Yensen & Tarifa 2003).

Conservation status. National, Data Deficient (DD); Global, Least Concern (LC).

Neogale frenata (Lichtenstein, 1831)

Material. None.

Locality. Ashigsho, Rancho Triste (41).

Identification. Dorsal coat dark chocolate brown (Fig. 18B), shiny and uniform. Pale orange chin and neck including belly. Tail robust and hairy with a black tip. Surface of soles of legs hairy (Sheffield & Thomas 1997).

Conservation status. National and Global, Least Concern (LC).

Remarks. This species was recently transferred to the genus *Neogale* by Patterson et al. (2021).

DISCUSSION

In Ecuador, only the Province de Pichincha has a published checklist of small non-volant mammals (Curay et al. 2019, see Supplementary Materials). This province is located in northwestern Ecuador, and its 9,536 km^2 area is home to 48 species, a richness similar to what we reported here for El Oro (46 spp.), although in a smaller area (5,767 km^2). Other areas in western Ecuador with important diversity are the Reserva Otonga (26 spp.) in Provincia de Cotopaxi (Jarrín-V 2001; Pinto et al. 2018; Lee et al. 2022), and Lita (23 spp.) in the Provincia de Imbabura (Curay et al. 2022). However, these two reserves are concentrated in territories smaller than 50 km^2.

The Equatorial-Pacific ecoregion is suffering an accelerated deforestation process (Curatola Fernández et al. 2015; Prieto-Torres et al. 2018; Kleemann et al. 2022). For example, in 2018 the fragmentation index increased by 11.6% in seasonal and semi-deciduous dry forests (Rivas et al. 2021). In El Oro the outlook is no more encouraging. Most of the ecosystems have been transformed into agricultural and livestock areas and now represent the main landscape matrix, with 52% of the total area of the province. This is of particular concern, as species with greater fragmentation have been shown to be at greater risk of extinction (Crooks et al. 2017).

The natural ecosystems with the greatest extension in the Provincia de El Oro are native forest and shrub veg-

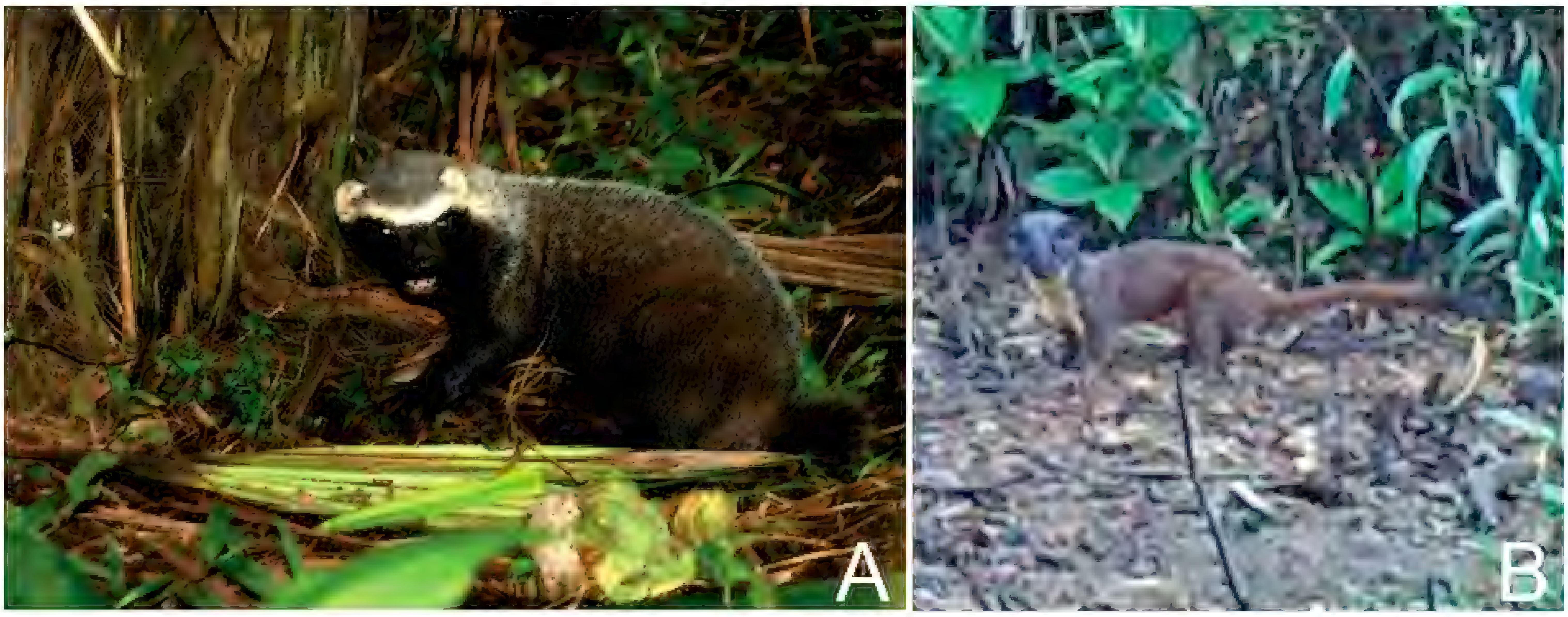

Fig. 18. A. Greater Grison, *Galictis vittata* recorded in the Reserva Buenaventura (Photo by J.C. Sánchez). **B**. Long-tailed Weasel, *Neogale frenata* recorded in the Ashigsho, Provincia de El Oro (Photo by J.L. Mena-Jaen).

etation, which together represent 31.65% of the territory. However, these ecosystems also represent the highest degree of fragmentation; for example, the native forest is fragmented in 2,403 patches (major patch index 11.8%), and shrub and herbaceous vegetation is even more fragmented in 2,546 patches (major patch index has a value of 19). Only the páramo, shrub and herbaceous vegetation show a low degree of fragmentation. Despite being fragmented ecosystems, they support an important richness of vertebrates, including 629 species of birds (Garzón-Santomaro et al. 2019b), 130 species of mammals (Brito et al. 2018; this study), 87 species of reptiles, and 50 species of amphibians (Yánez-Muñoz et al. 2019).

Furthermore, in the Province de El Oro, the highest concentration of richness (35 spp.), as well as endemic (6 spp.) and threatened (10 spp.) species of small non-volant mammals are found in native forest and shrub vegetation (Fig. 2A). Unfortunately, these ecosystems are suffering constant anthropogenic pressure, so that, for example, the seasonal piedmont forest has been categorized as an Endangered Ecosystem (Noh et al. 2020). In El Oro, only the coastal ecosystem (2% of the province's surface area) represented by the Reserva Ecológica Arenillas is protected, although it appears that the conservation of state protected areas is not guaranteed in the future either (Kleemann et al. 2022). Despite the above, united conservation of habitats is important to protect representative ecosystems, such as the piemontane forest and montane forest. In addition to maintaining biological diversity, these ecosystems protect the water sources that supply all the cities in the province.

Due to the rapid conversion of natural habitat, it is crucial to carry out inventories to catalog the species in each political jurisdiction (local, provincial, national, and regional) as well as determine their systematic identification, geographic distribution, and ecological function. This information is fragmentary, incomplete, and outdated in most countries of the world (Voss and Emmons 1996; Bauni et al. 2021). Ecuador is no exception; despite being one of the countries with the smallest territories in South America, there are still numerous areas with information gaps (Kleemann et al. 2022). This lack of information is evident in the coastal region between the provinces of Manabí and El Oro. Although the diversity of small non-volant mammals has been reported since 1860 (Thomas, 1899), few subsequent inventories have been conducted (Emmons & Albuja 1992; Bravo-Salinas et al. 2021), and other spot reports (e.g., Anderson & Jarrín-V 2002; Brito et al. 2015; Brito-Vera et al. 2022). Unfortunately, extensive habitat conversion along the Ecuadorian coast makes it unlikely that lowland forests can be effectively sampled for small non-volant mammals, but better opportunities may exist in the Cordillera Chongón-Colonche.

Finally, the diversity of small non-volant mammals in the Provincia de El Oro will not remain static for long. Numerous species constitute species complexes (e.g., "*Handleyomys*", *Oecomys*, *Oreoryzomys*, *Proechimys*, *Rhipidomys*, *Thomasomys* and *Transandinomys*; see Patton et al. 2015), which are waiting to be resolved. The use of integrative taxonomy might be the appropriate way to address these taxa.

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Spread of the invasive Giant Asian Mantis *Hierodula tenuidentata* Saussure, 1869 (Mantodea: Mantidae) in Europe with new Hungarian data

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Abstract. The Giant Asian Mantis (*Hierodula tenuidentata*) has a rapid spread in Europe that is considerably helped by global trade and transportation. Following the expansion of this species is crucial to understand the factors facilitating its success. In this paper, we present the first 103 Hungarian observations (42 sites) of *H. tenuidentata i*ncluding its currently known northernmost established population in Central Europe. We also provide its mapped, published and unpublished citizen science-based European data from the 1910s to 2022 highlighting the main dynamics and areas in the spread of this species here. The potential ways of the spread of *H. tenuidentata*, its habitat characteristics and some possible impacts on the native European fauna are also discussed based on previous assumptions and recent experiences.

Key words. Invasion, citizen science, urban heat island, distribution, Hungary, conservation.

INTRODUCTION

Alien species have an increasing number worldwide which largely originates from the growth of global trade and transportation (Hulme 2021). Recently more and more papers are published on this topic (Kühn et al. 2011) even with the use of citizen science data and methods which have an important and growing role in mapping alien species (Encarnação et al. 2021; Wallace et al. 2021)

In Europe this kind of data source is used to capture and map non-native insects, like praying mantises (e.g., Moulin 2020; van der Heyden & Schwarz 2021). The number of alien mantid species and some of their populations in Europe increased recently like in the case of *Sphodromantis viridis* Forskal, 1775, *Hierodula patellifera* Serville, 1839 or even more conspicuously in the case of *Hierodula tenuidentata* Saussure, 1869 (Schwarz & Ehrmann 2018; Battiston et al. 2020). In recent publications, *H. tenuidentata* is sometimes referred to as *H. transcaucasica* Brunner von Wattenwyl, 1878. According to Battiston et al. (2018), the previously used character to separate these two species, the colour of the discoidal spines of the fore femora, proved to be invalid. The comprehensive morphological comparison of their male genitalia also did not bring any appreciable differences (Battiston et al. 2018), however, this approach is widely used in the systematic of insects (Song & Bucheli, 2010) such as mantids (Brannoch & Svenson 2016). Thus, in this article, we follow the statement of Battiston et al. (2018) and account for *H. transcaucasica* as a synonym of the formerly described *H. tenuidentata* as it was previously raised by other authors too (Ehrmann 2011; Ehrmann & Borer 2015).

The Giant Asian Mantis *H. tenuidentata* has a wide distribution from Southeast Asia on the east that extends partly to Europe in the west (Shcherbakov & Battiston 2020), containing some regions of Azerbaijan, Georgia and the southernmost parts of European Russia and Ukraine (Werner 1916; Ramme 1951; Battiston & Massa 2008; Ehrmann 2011). The westernmost known locality of *H. tenuidentata* before the twenty-first century in Europe was in Crimea, Ukraine. After this species was mentioned from there by Werner in 1916, it was not observed there until its rediscovery in the early 2000s (Pushkar &

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Kavurka 2016). According to the published data arranged by time, this mantid was first observed west of Crimea in Greece in 2007 (Cianferoni et al. 2018) and in the following years it began to spread locally (Schwarz & Ehrmann 2018; van der Heyden 2018a; Romanowski et al. 2019; van der Heyden & Schwarz 2021) such as in Ukraine, mainly near the shoreline of the Black Sea but also towards the interior of the country (Pushkar & Kavurka 2016; Bronskov & Filchakova 2022). In 2016, *H. tenuidentata* was first recorded in another Mediterranean area, the Po Valley, Italy (Battiston et al. 2018), where it successfully established and began a rapid spread (Cianferoni et al. 2018; Di Pietro & Battiston 2021). After 2017, *H. tenuidentata* was observed in other Balkanian countries like Bulgaria (Romanowski et al. 2019; Zlatkov et al. 2020), North Macedonia (Cianferoni et al. 2018), Albania (van der Heyden 2018b; Romanowski et al. 2019), Serbia (Vujić et al. 2021), Slovenia (van der Heyden 2021), Bosnia and Herzegovina (Kulijer et al. 2022), Croatia (Martinović et al. 2022) as well as in Romania (Pintilioaie et al. 2021), Austria (Essl & Zuna-Kratky 2021), France (Moulin & Rouard 2023) and Spain (van der Heyden 2021).

According to the recent spread of *H. tenuidentata* in Europe, it was expected to appear at least in the southern parts of Hungary as well (Vujić & Ivković 2023). In this paper, we provide the available observations from Hungary and the currently known distribution and spread in Europe based on published and new citizen science data with the summarisation of its possible effects on the native fauna and the ways of its spread, containing previous experiences.

MATERIAL AND METHODS

Spread in Europe

To map the spread of *H. tenuidentata* in Europe besides the Hungarian data we used the available observations of the adults, nymphs and oothecae from the website Gbif.org, focusing on the localities west of the 37th meridian east (the eastern border of Crimea). On Gbif.org, *H. tenuidentata* and *H. transcaucasica* belong to two different species pages. Due to their synonymy, we applied the database of *H. tenuidentata* (GBIF 2022a) and also of *H. transcaucasica* (GBIF 2022b). The identifications that were executed by the users of the source website were verified by the authors as well. The published localities of *H. tenuidentata* from the following papers (from 1910s to 2022) were also plotted: Pushkar & Kavurka 2016; Battiston et al. 2018; Cianferoni et al. 2018; Schwarz & Ehrmann 2018; van der Heyden 2018a; van der Heyden 2018b; Romanowski et al. 2019; Zlatkov et al. 2020; Di Pietro & Battiston 2021; Essl & Zuna-Kratky 2021; Pintilioaie et al. 2021; van der Heyden 2021; Vujić et al. 2021; Brosnkov & Filchakova 2022; Kulijer et al. 2022; Martinović et al. 2022; van der Heyden & Schwarz 2021.

Hungarian data

Distributional data of *H. tenuidentata* from Hungary was collected from different sources. Some of the individuals were observed in the field by direct search in previously known or possible locations. We also applied citizen science data from izeltlabuak.hu which is the largest Hungarian website for collecting mainly distributional and phenological data about the arthropod fauna of Hungary. There are several Hungarian Facebook groups where nature and insect lovers can upload their observations to ask for identification or just to share their experiences. These data were also collected. In 2022 there was an appeal of the people of Szeged and Kiskunhalas (Southern Hungary) to share their observations of *H. tenuidentata* via a local news site and a Facebook page. We accepted only those data that were confirmed with at least one photo of the individual from which its identification was possible.

Identification of the individuals was based on the key and figures published by Battiston et al. (2019) and Pintilioaie et al. (2021). Considering these characteristics, the observed *H. tenuidentata* specimens were clearly distinguishable from the congeneric species *H. patellifera* by the lack of the whitish basal plates under its coxal spines on the forelegs, from *S. viridis* by its shorter pronotum with less prominent supracoxal dilatation, and by the whitish stigma on its forewing from other similar mantid species in Europe just like from *Mantis religiosa* (Linnaeus, 1758), the only native praying mantis species in Hungary. In those two cases where male individuals were captured (from Budapest and Zákányszék), the morphology of the genital structures was also examined and compared to the figures published in Battiston & Massa (2008), Battiston et al. (2020) and Liu et al. (2021). The photos of the genital structures were taken with Euromex C-MEX 10 Pro camera and were stacked with Image Focus Alpha software. The collected male and female individuals were preserved and placed in the collection of the Hungarian Natural History Museum.

RESULTS

Spread in Europe

For mapping the spread of *H. tenuidentata* in Europe, 180 published and 1331 other unpublished data were collected, including Hungarian records. The number of observations of individuals and oothecae is showing a significant increase year by year throughout Europe, particularly in areas where this species probably had its earliest established populations: along the northern part of the Black

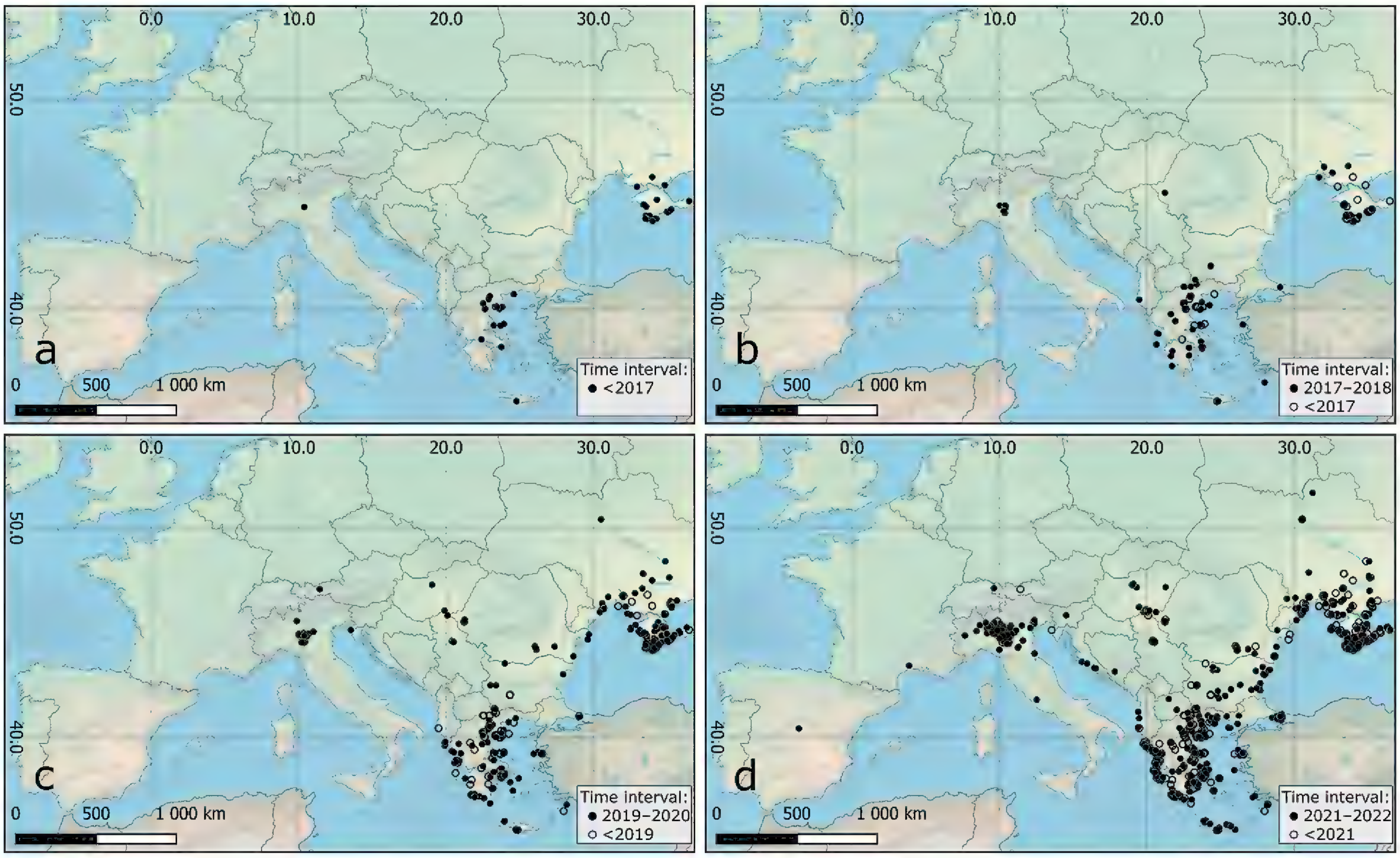

Fig. 1. Spread of the invasive mantid *Hierodula tenuidentata* in Europe, west of the 37th meridian east. Maps are based on its published observations, and new citizen science based records from Hungary and Gbif.org. Solid circles: observations from the plotted time interval. Empty circles: former observations with no data from the plotted time interval.

Sea coast, in the Southern parts of the Balkan Peninsula and in the Po Valley in Italy (Fig. 1).

Hungarian observations

The first observation of *H. tenuidentata* from Hungary was in 2019 in Zákányszék (South Hungary) in a garden. In the following years, larvae, adult individuals and hatched oothecae were also found here. Similar records were reported from several other settlements nearby Szeged (South Hungary), from Kiskunhalas (South Hungary, Fig. 2) and from Budapest (Central Hungary). A few single observations are also known from Hungary without evidence of local establishment there.

Until the end of 2022, altogether 103 observations (88 adult individuals, 8 larvae and 7 oothecae) of *H. tenuidentata* were confirmed in Hungary which are presented here (Fig. 3; Appendix I: Table 1). Altogether, the Hungarian observations came from 42 different localities, mostly gardens or other residential areas (79%; n = 33), less industrial parks (7%), garden centres and cemeteries (5% each), park and goose farm (each 1%). The collected and examined male individuals were also identified as *H. tenuidentata* which was confirmed by the morphology of their genital structures besides other characteristics (Fig. 4).

DISCUSSION

Distribution in Hungary and Europe

Along with other countries in Europe, *H. tenuidentata* has been recorded also in Hungary where it was first observed in 2019 (Zákányszék, South Hungary). In the following years, more and more individuals appeared in two main sites: in Budapest (Central Hungary) which is currently known to be the northernmost stable occurrence of *H. tenuidentata* in Central Europe, and in Szeged (South Hungary) with the nearby settlements (e.g., Zákányszék). Not only adult individuals were found in the same localities in consecutive years but larvae and hatched oothecae as well, from which we can conclude established populations in some Central and Southern Hungarian areas (Fig. 3).

The case is similar in many other parts of Europe where this species was introduced and successfully established (Fig. 1). Its rapid expansion in the Po Valley, Italy (Di Pietro & Battiston 2021) and in the Balkan Peninsula (Kulijer et al. 2022) is remarkable, however, there are grey spots in the latter one without any records, like the area of Kosovo and Montenegro but according to the current range of *H. tenuidentata*, it is probable that this species occurs here as well. There are also many single observations in Europe with no data from the certain

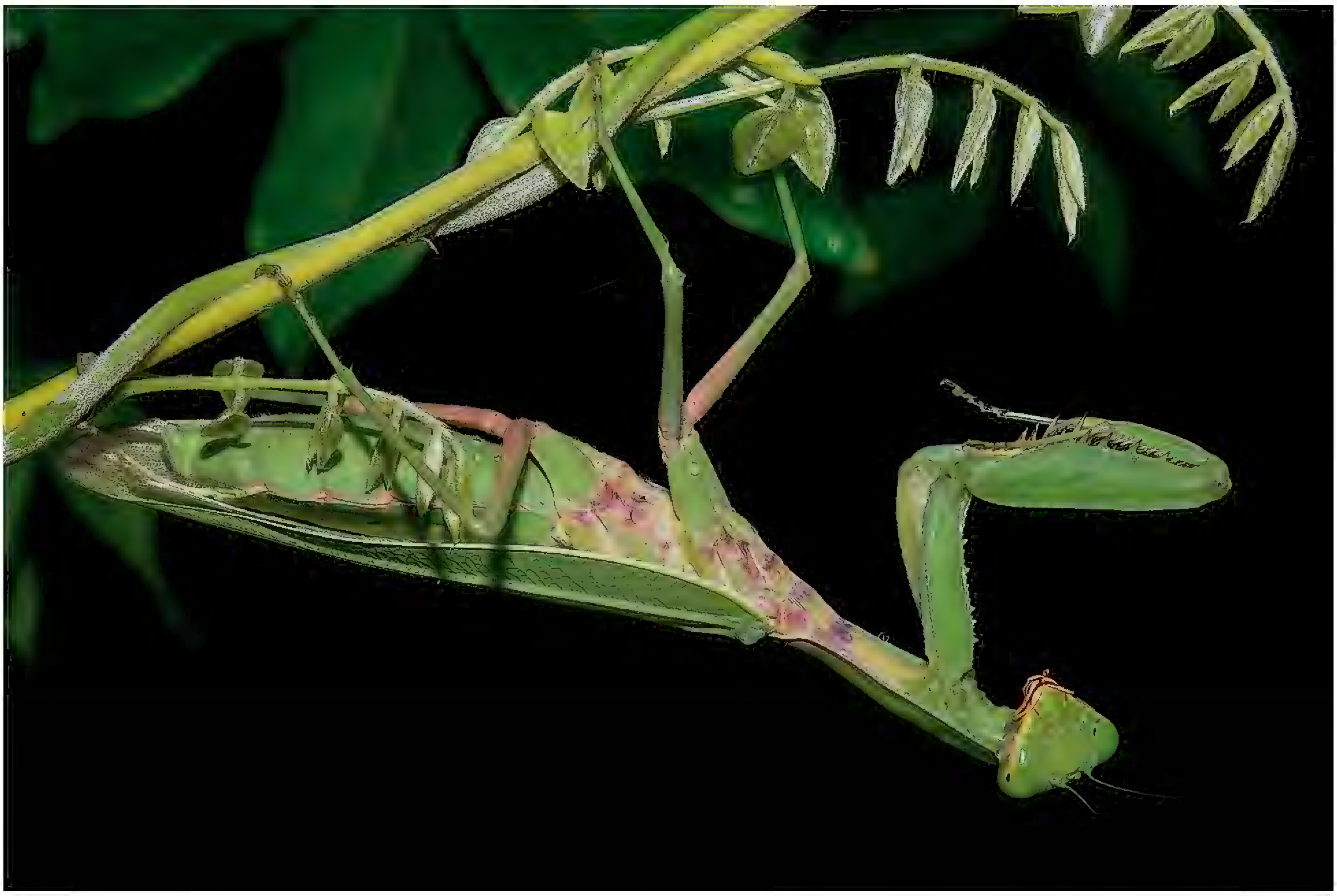

Fig. 2. Adult female of *Hierodula tenuidentata* (Kiskunhalas; 46.4482° N, 19.4817° E; South Hungary; 1 Sep. 2022). Photo by Tamás Kiss.

locality from different years (e.g., Essl & Zuna-Kratky 2021) which can be due to introductions without establishments or even the unnoticed low number of individuals in the initial phases of establishments (Kulijer et al. 2022).

For alien insect species, mainly if they are adapted to a warmer climate, cold winter temperatures seem to be one of the most important abiotic limiting factors regarding their establishment (Bale 2002). In Europe, it can primarily determine their northern range edges (Orlova-Bienkowskaja et al. 2020), which is visible in the case of *H. tenuidentata* as well. So far, the northernmost known single observation of this species in Europe, has been recorded in Chernihiv [51.5°N, 31.2°E], Ukraine (Fig. 1). The cold winters here can make the establishment of this species a challenging issue, however, it is already surviving in some Hungarian and Serbian settlements inside the Pannonian Basin where the winters can also be severe (Gavrilov et al. 2020; Vujić et al. 2021). The urban heat island effect in these populated areas definitely can help the survival of *H. tenuidentata* similar to other alien species (Gaertner et al. 2016). Most of the individuals of *H. tenuidentata* in Europe were observed in settlements mainly in lower latitudes with moderate climates. However, the effects of climate change and the strengthening potential source populations in the south can support the northward spread of this species (Chen et al. 2011; Rimšaitė et al. 2022).

It is important to consider that in the case of citizen science-based species distribution data like this, there is always a bias: highly populated areas are usually overrepresented and other sites with fewer people are underrepresented (Boakes et al. 2010; Wallace et al. 2021). However, the settlement close observations of *H. tenuidentata* in Europe could probably form a valid pattern explained by the possible climatic needs of this species and the dense transport linkages that could facilitate its introductions here (Gaertner et al. 2016).

Ways of spread

Behind the rapid spread of *H. tenuidentata* in Europe, climate change and human activities like transportation and trade can be the two main driving forces. The reappearance of *H. tenuidentata* in Crimea in the early 2000s can possibly be due to an active range expansion from the Caucasus, which could be favoured by climate change such as the northward spread of this species in Ukraine from the eastern coast of the Black Sea (Pushkar & Kavurka 2016). However, its appearance in several different

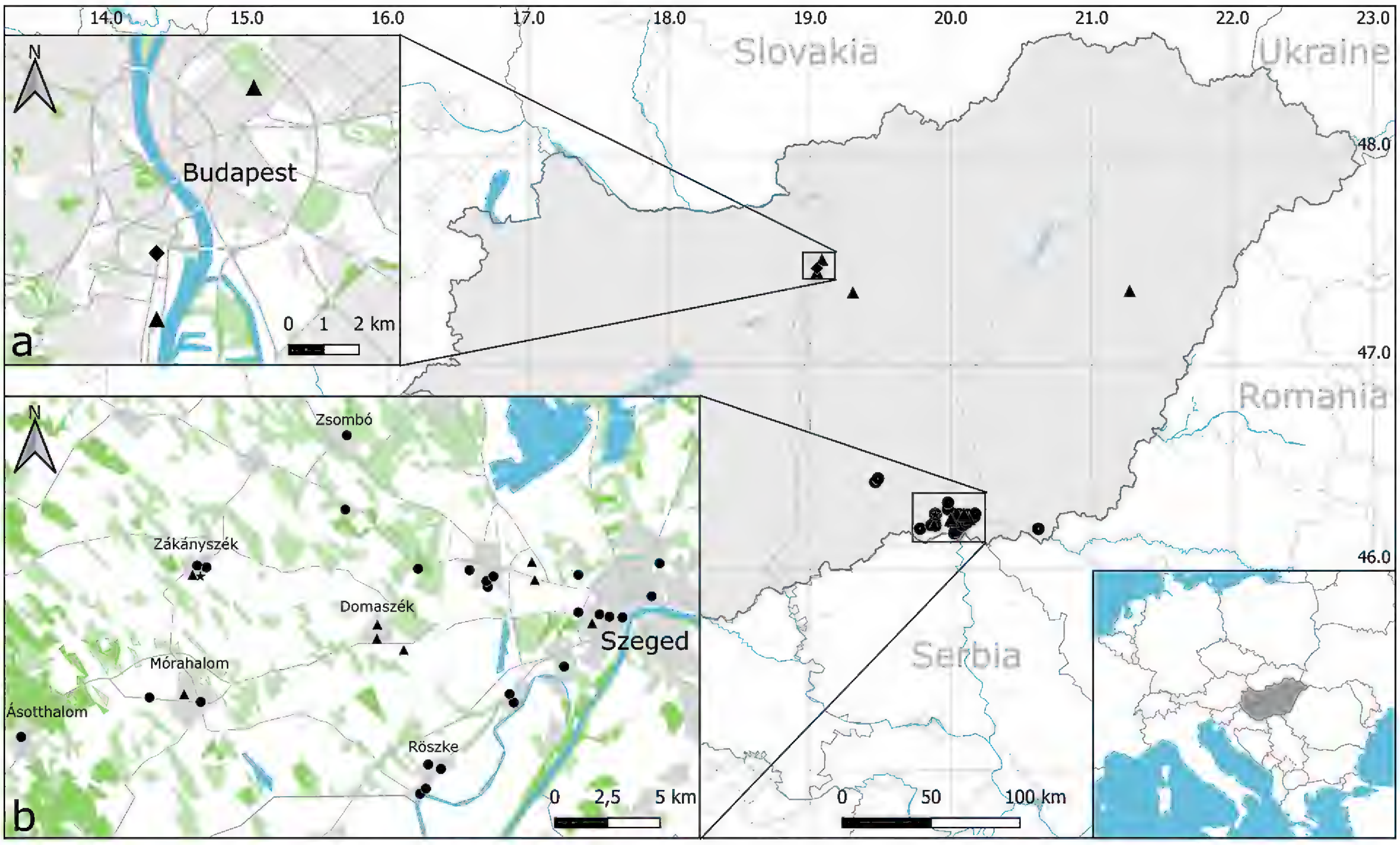

Fig. 3. Localities of the observed *Hierodula tenuidentata* individuals and oothecae in Hungary. Enlarged observation sites in a, Budapest b, Szeged with nearby settlements. The year of the first record from a specific locality is presented as a star (2019), rectangle (2020), triangle (2021) or circle (2022). Basemap: OpenStreetMap (https://openstreetmap.org/copyright).

settlements hundreds of kilometres apart from each other within a short time interval cannot be explained only by active expansion, but by human introductions (Pintilioaie et al. 2021).

There are several possibilities for introducing a non-native species intentionally or unintentionally. Deliberate release or escape of exotic pets is one of them (Hulme 2015). However, some praying mantis species became popular pets and have a general trade in Europe (Battiston et al. 2022), *H. tenuidentata* is not a commonly reared species here, thus its origin from captive breedings seems unlikely (Battiston et al. 2018, Halász 2022). The arrival of *H. tenuidentata* in several parts of Europe could probably happen through mercantile channels by multiple introductions as stowaways (Hulme 2015; Battiston et al. 2018; Cianferoni et al. 2018; Pintilioaie et al. 2021).

Oothecae laid on manufactured goods, ornamental plants, vehicles, timber or other material can easily be transferred by human trade and transportation far from its origin (Pushkar & Kavurka 2016; Cianferoni et al. 2018). Potentially around a hundred larvae can hatch from one ootheca, but in nature, this number can be reduced to a few tens of hatched individuals due to parasitoids or suboptimal microclimatic conditions (Mirzaee et al. 2021; Mirzaee et al. 2022). Long-lived females of this species usually lay five oothecae (Mirzaee et al. 2021) thus both introduced fertile females and oothecae can be considered as high propagule pressure that is very likely to have an important role in the rapid spread of *H. tenuidentata* in Europe (Lockwood et al. 2005). Records of this species in garden centres (e.g., Martinović et al. 2022), sites with newly planted shrubs and trees (e.g., Budai Wlazer residential park and Városliget, Budapest, Hungary), industrial parks with timber and other material trade (e.g., Délép Industrial Park Kft., Szeged, Hungary) support the importance of these pathways in the spread of *H. tenuidentata* such as its early appearance far from the East, in the Po Valley, Italy which is known to be one of the biggest ornamental plant transporter countries in Europe (Eurostat 2017).

It is also notable that the adults of this species are capable of flight, sometimes overcoming large distances (Pushkar & Kavurka 2016) which provides other opportunities in their spread even naturally (e.g., by wind, Cianferoni et al. 2018) or mediated by humans. Specimens attracted by the lights of transport vehicles like ships could be transferred to other ports crossing a stretch of the sea (Cianferoni et al. 2018). It possibly helped the spread of *H. tenuidentata* around the Black Sea coast (Moulin 2020; Pintilioaie et al. 2021).

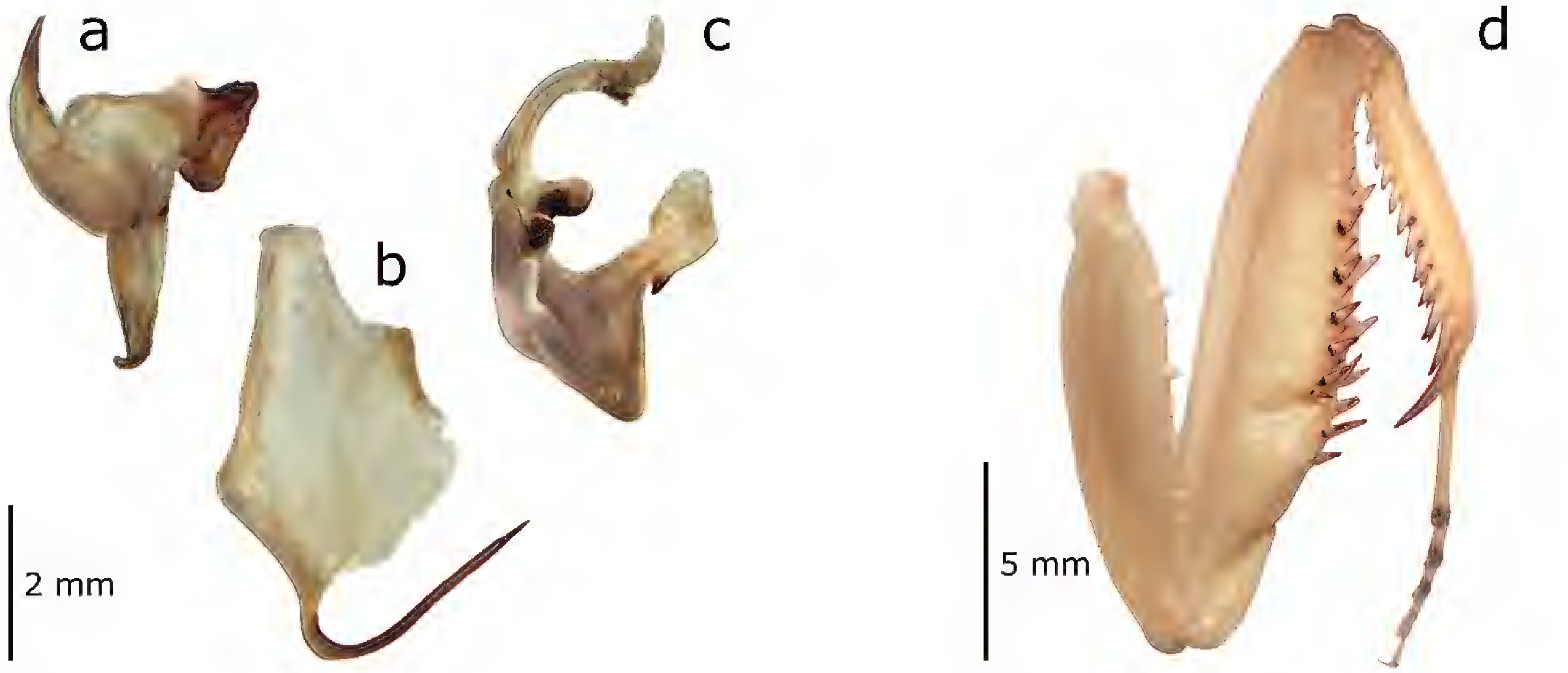

Fig. 4. Morphological characters of a male *Hierodula tenuidentata* collected in Zákányszék [46.27° N, 19.89° E], South Hungary, 30 Sep. 2022. **a**. Left phallomere. **b**. Ventral phallomere. **c**. Right phallomere. **d**. Left foreleg.

Habitat use

The Giant Asian Mantis is known to be a primarily arboreal mantid species which is usually found in forests and shrub vegetations in its original distribution from Southeast Europe to Southeast Asia (Pushkar & Kavurka 2016; Shcherbakov & Battiston 2020). Introduced individuals in Europe within settlements were found on tree canopies, trunks, shrubs and walls or other vertical surfaces that represent their original habitats (Romanowski et al. 2019; Kulijer et al.2021; Pintilioaie et al. 2021). Despite the large size of *H. tenuidentata*, its mainly arboreal life strategy could make it harder to detect its newly established populations with a small number of individuals. It seems that imago females are easier to observe than imago males or nymphs which can be due to their longer lifespan (Mirzaee et al. 2022) or even due to their oothecae laying habits when they possibly climb down to deposit their egg cases at lower heights where they can be captured easier (Pintilioaie et al. 2021). Hungarian data also support this as most of the observed individuals were adult females (80%, n = 77) less males (12%) and nymphs (8%).

As mentioned by Pintilioaie et al. (2021), females of *H. tenuidentata* probably prefer smoother surfaces for laying oothecae. According to their observations, the number of egg cases found in Romania on *Platanus* sp. trunks and twigs was overrepresented compared to other plant species with more rough trunks. In the Budapest park Városliget [47.5097° N, 19.0851° E], our observations also support this assumption. However, no oothecae were found yet in Városliget, most of the adult females were recorded here on the trunks of *Platanus* sp. It is important to note that plane trees are a more abundant species here than in the observation sites in Romania according to Pintilioaie et al. (2021).

Possible impacts and heterospecific patterns of such alien species

Invasive species are capable of causing environmental or economic harm (Iannone et al. 2021), however, forecasting these impacts is a great challenge (Dick et al. 2013). In the case of *H. tenuidentata*, its recent arrival and the low number of ecological studies in Europe (e.g., Pintilioaie et al. 2022) make it even harder to make valid predictions about the possible effects of this predatory species on the native fauna.

The survival of *H. tenuidentata* in Europe seems to be facilitated by the urban heat island effect and the occurrences of this species here are mainly restricted to settlements or their close surroundings and only a few of them occur in natural habitats (Pintilioaie et al. 2020). This distributional pattern can moderate the potential effects of *H. tenuidentata* on the native fauna, partly on other mantis species. However, in Europe, the widespread *Mantis religiosa* also has well-established populations in urban areas (Battiston 2016). The predatory behaviour of these two species and their overlapping range and life cycle can lead to possible interference between them (Battiston et al. 2018). *H. tenuidentata* is known to be an arboreal species living in higher layers of vegetation, while *M. religiosa* usually inhabits mainly grasslands (Battiston 2016) which possibly lowers the chance of competition or predation between them. However, it is known that *M. religiosa* males can be attracted by the sexual pheromones of other mantid species (Lelito & Brown 2008). Due to this phenomenon, *H. tenuidentata*

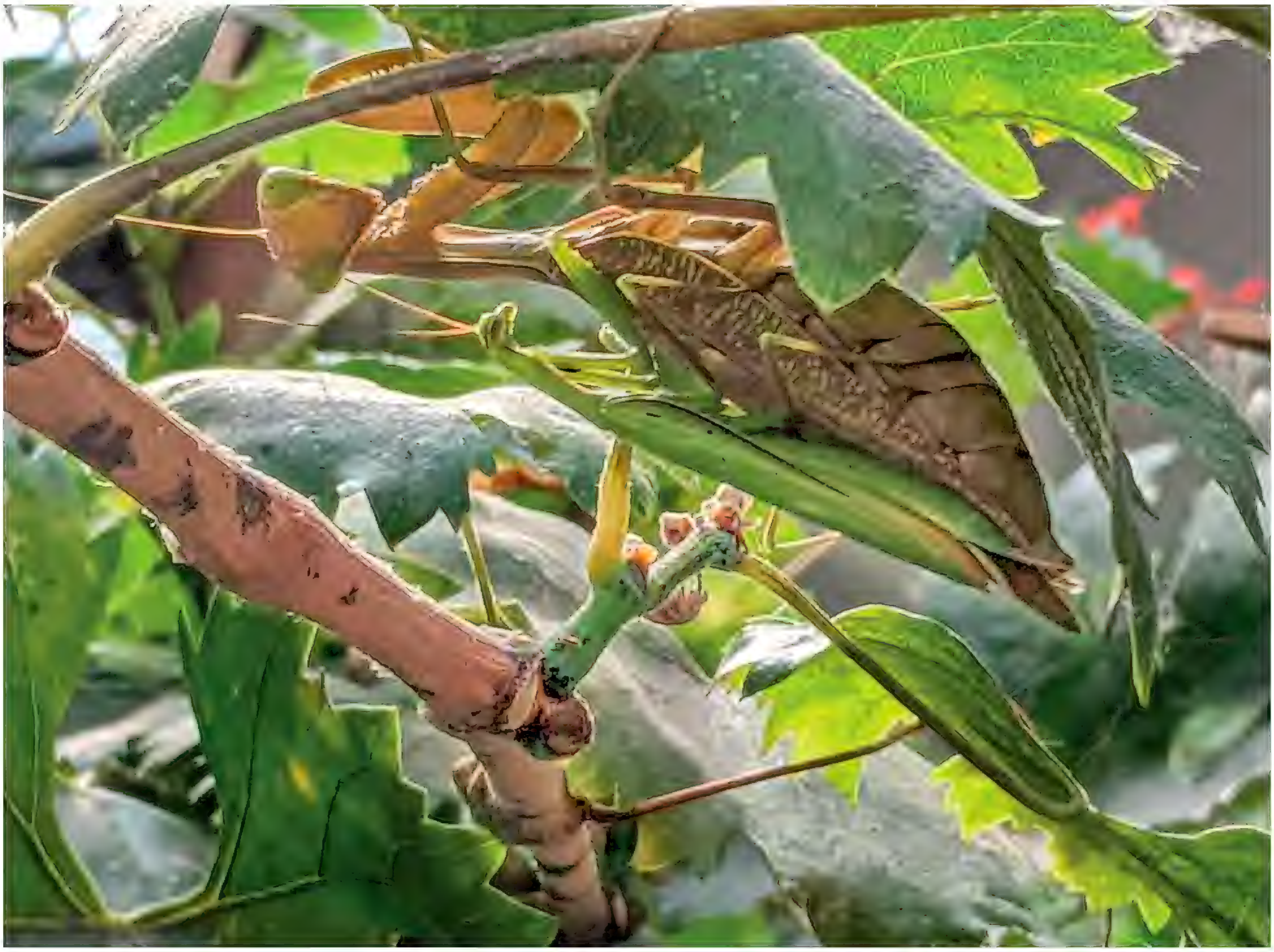

Fig. 5. Mating behaviour of a male *Mantis religiosa* with a female *Hierodula tenuidentata* (Zákányszék; 46.27° N, 19.89° E; South Hungary). Photo by Balázs Torma.

females can potentially lower the reproduction success of *M. religiosa* males in their close habitats by attracting them and being a threat to the native species due to the sexually cannibalistic behaviour of *H. tenuidentata* (Fea et al. 2013; Battiston et al. 2018). This assumption is supported by a documented Hungarian observation in Zákányszék (South Hungarian) as well, where a male *M. religiosa* tried to copulate with a female *H. tenuidentata* from a well-settled population of the latter (Fig. 5).

Besides this example, there are several other possible opportunities for this invasive mantid to affect some of the native species negatively (Crowder & Snyder 2010) or even positively (Mirzaee et al. 2021; Rădac & Háva 2021). The exact impacts of *H. tenuidentata* on European ecosystems are still not known (Battiston et al. 2018), but further ecological studies and the essential help of citizen scientists can lead us closer to effective conservational steps against biological invasions (Encarnação et al. 2021; Pintilioaie et al. 2022).

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APPENDIX I

(*electronic supplement, available at www.zoologicalbulletin.de*)

Table 1 (continued next two pages)**.** Hungarian observations of Hierodula tenuidentata until the end of 2022. For each record, the following pieces of information are given after the settlement name: geographical coordinates in decimal degrees with two digits (if only the name of the settlement is known) or with four digits (if at least the name of the road is known), observation date, number, sex and life stage of the individual(s) (O = ootheca; L = larvae; none = adult; collector or photographer, source: FB = Facebook groups; IL = izeltlabuak.hu; PA = public appeal; none = other). The records are arranged in alphabetical order of the settlements. Individuals that were preserved and placed in the collection of the Hungarian Natural History Museum are marked (*).

Locality	Observations
Apátfalva [46.2002° N, 20.6204° E]	9.X.2022, 5 ♀♀, János Dombi, PA
Ásotthalom [46.2017° N, 19.7798° E]	6.X.2022, 1 ♀, ”kved98”, IL
Bordány [46.2985° N, 19.9790° E]	17.X.2022, 1 ♀, Tata Papp, PA
Budapest [47.4676° N, 19.0486° E]	5.X.2020, 1 ♀*, Kurszán Gál, FB
	23.IX.2021, 1♀, Kurszán Gál
	5.XI.2021, 2 ♀♀, Kurszán Gál, FB
	8.VIII.2022, 1 ♀L, Kurszán Gál, FB
	4.X.2022, 1 ♀, Kurszán Gál, FB
Budapest [47.4509° N, 19.0461° E]	30.IX.2021, 1 ♂*, Kurszán Gál, FB
Budapest [47.5097° N, 19.0851° E]	2.IX.2021, 1 ♀L, Eduardo Balogh, FB
	8.IX.2021, 1 ♀, Klári Adrienn Szitási, FB
	31.X.2021, 6 ♀♀ [2 ♀♀*], Attila László Péntek
	1.XI.2021, 2 ♀♀, Kurszán Gál, IL
	24.IX.2022, 1 ♀, Eduardo Balogh, FB
Domaszék [46.2496° N, 19.9988° E]	9.IX.2021, 1 ♀, Erzsébet Mészáros, PA
Domaszék [46.2436° N, 19.9985° E]	28.X.2021, 1 ♀, Gábor Janzsó, FB
	1.X.2022, 1 ♂, 1 O, Gábor Janzsó
	12.XI.2022, 1 ♂, Bálint Janzsó
Domaszék [46.2388° N, 20.0150° E]	30.X.2021, 1 ♀, Lili Lajtár, IL
	15.VI.2022, 1 ♀L, Lili Lajtár, IL
	16.VII.2022, 1 ♀L, Lili Lajtár, IL
	7.VIII.2022, 1 ♀, Lili Lajtár, IL
	15.VIII.2022, 1 ♀, Lili Lajtár, IL
	18.VIII.2022, 1 ♂, 1 ♀, Lili Lajtár, IL
	19.VIII.2022, 1 ♂, Lili Lajtár, IL
	25.VIII.2022, 1 ♂, Lili Lajtár, IL
	29.VIII.2022, 1 ♂, Lili Lajtár, IL
	31.VIII.2022, 1 ♂, Lili Lajtár, IL

Table 1 (continued).

Locality	Observations
	1.IX.2022, 1 ♀, Lili Lajtár, IL
	27.IX.2022, 1 ♀, Lili Lajtár, IL
Kaba [47.36° N, 21.27° E]	19.07.2021, 1L, Annamária Dámóczi, FB
Kiskunhalas [46.4482° N, 19.4817° E]	1.IX.2022, 1♀, Tamás Kiss, IL
	23.X.2022, 3 ♀♀, Viktor Greguss
	29.X.2022, 1 O, Viktor Greguss
Kiskunhalas [46.4314° N, 19.4631° E]	27.X.2022., 1 ♀, Regina Fejes, PA
Mórahalom [46.22°N, 19.88°E]	31.VII.2021, 1 ♀L, Orsolya Nagy, FB
Mórahalom [46.2167°N, 19.8902°E]	7.X.2022, 1 ♀*, Attila László Péntek
	8.X.2022, 1 ♀, Attila László Péntek
Röszke [46.19° N, 20.03° E]	VIII.2022., 1 ♀, Gergely Bérdi, FB
Röszke [46.1775° N, 20.0250° E]	8.X.2022, 1 ♀, Barbara Vörös, PA
Röszke [46.1881° N, 20.0378° E]	8.X.2022, 2 ♀♀ [1 ♀*], Attila László Péntek
Röszke [46.1797° N, 20.0285° E]	24.X.2022, 1 ♀, ”BHD-91”, IL
Szeged [46.2501° N, 20.1308° E]	1.X.2021, 1 ♀, Izabella Zombori-Benczur, FB
Szeged [46.2685° N, 20.0954° E]	27.X.2021, 1♀, Tibor Csende, FB
	12.VII.2022, 1 ♀L, Tibor Csende, FB
Szeged [46.2548° N, 20.1223° E]	7.X.2022, 1 ♀, Lénárd Biacs, PA
	25.X.2022, 1 ♀, Áron Kovács, FB
Szeged [46.2529° N, 20.1414° E]	12.X.2022, 1 ♀, László Garai Szakács, IL
Szeged [46.2526° N, 20.1494° E]	15.X.2022, 1 ♀, Andrea Péntek, PA
Szeged [46.2756° N, 20.1722° E]	15.X.2022, 1 ♀, Gábor Szabó, PA
Szeged [46.2539° N, 20.1353° E]	16.X.2022, 1 ♀, Zsuzsanna Hangai, FB
Szeged [46.2707° N, 20.1223° E]	17.X.2022, 1 ♀, ”Brigitta90”, IL
Szeged [46.2317° N, 20.1136° E]	20.X.2022, 1 ♀, Imréné Szabó, PA
Szeged [46.2616° N, 20.1673° E]	22.XI.2022, 1 ♀, Ábel Torma
Szeged-Kiskundorozsma [46.27° N, 20.07° E]	3.XI.2022, 1 ♀, Katalin Harnóczi
Szeged-Kiskundorozsma [46.2762° N, 20.0936° E]	11.X.2021, 1 ♀, Barna Bálint Tőkés , FB
	12.VIII.2022, 1♀, Barna Bálint Tőkés
	9.X.2022, 2 ♀♀ [1♀*], Barna Bálint Tőkés
Szeged-Kiskundorozsma [46.2727° N, 20.0553° E]	13.VIII.2022, 1 ♂, Attila Ungi, PA
Szeged-Kiskundorozsma [46.2680° N, 20.0658° E]	8.X.2022, 1 ♀, Beáta Milankovicné Mészáros, PA

Table 1 (continued).

Locality	**Observations**
Szeged-Kiskundorozsma [46.2733° N, 20.0238° E]	16.X.2022, 1 ♀, Marietta Ábel, IL
Szeged-Kiskundorozsma [46.2656° N, 20.0665° E]	17.X.2022, 1 ♀, Tamás Ungi, PA
Szeged-Szentmihály [46.22° N, 20.08° E]	11.X.2022, 1 ♀, Katalin Harnóczi
	16.X.2022, 1 ♀, Erika Csatlósné Tóth, PA
Szeged-Szentmihály [46.2164° N, 20.0825° E]	17.X.2022, 1 ♀, Zoltán Szűcs, PA
Üllő-Pusztalöb [47.3515° N, 19.3041° E]	28.IX.2021, 1 ♀, Kristóf Teszárs, FB
Zákányszék [46.27° N, 19.89° E]	28.XI.2019, 1 ♀, Balázs Torma, PA
	11.IX.2020, 1 ♂, 1 ♀, Balázs Torma
	13.VII.2021, 3 O, Balázs Torma
	14.VII.2021, 2 O, Balázs Torma
	4.IX.2021, 1 ♀, Balázs Torma
	9.IX.2021, 1 ♀, Balázs Torma;
	19.IX.2021, 1 ♀, Balázs Torma
	29.IX.2022, 2 ♀♀, Balázs Torma
	30.IX.2022, 1 ♂, Balázs Torma
	9.X.2022, 1 ♀, Balázs Torma
Zákányszék [46.2707° N, 19.8852° E]	31.X.2021, 1 ♀, Károly Ábrahám, FB
Zákányszék [46.2746° N, 19.8880° E]	8.X.2022, 1 ♀*, Attila László Péntek
Zákányszék [46.2739° N, 19.8937° E]	16.X.2022, 1 ♀, István Agócs, PA
Zsombó [46.33° N, 19.98° E]	1.VIII.2022, 1 ♀, Tamás Győri

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Research article

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A new species and a new record of the jumping spider genus *Phintella* Strand, 1906 (Araneae: Salticidae) from the Central Highlands of Vietnam

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Abstract. A new jumping spider species, *Phintella daklak* Hoang sp. nov. (♂♀) is described and illustrated from the Central Highlands, Vietnam. Additionally, the species *P. sancha* Cao & Li, 2016 is reported for the first time in Vietnam, from a male specimen. To date, a total of nine species of the genus *Phintella* Strand, 1906 have been recorded for the country.

Keywords. Dak Lak, description, speciose, transfer, Oriental region.

INTRODUCTION

The genus *Phintella* Strand, 1906 is one of the most speciose genera of Salticidae, with currently 70 species mainly found in the Oriental region, and a few in the Palaearctic and Afrotropical regions (Logunov 2021; World Spider Catalog 2023). However, more than half of these species were previously assigned to other genera before being transferred to *Phintella* (World Spider Catalog 2023).

The first species of the genus *Phintella* recorded in Vietnam was *P. argenteola* (Simon, 1903) ex. *Telamonia* from Phuc Son, Nghe An Province (Simon, 1903) (now known as Phuoc Son District, Quang Nam Province, as noted by Hoang et al. 2023). After being long neglected, the salticid fauna in Vietnam was first revised by Żabka (1985), who reported nine species of *Phintella* in the country, of which one was later recognized to be a synonym (Luong et al. 2016) and another was transferred to *Chinattus* (Logunov 1999). Currently, the genus is represented by seven species in Vietnam: viz., *P. aequipeiformis* Żabka, 1985; *P. accentifera* (Simon, 1901); *P. argenteola* (Simon, 1903); *P. bifurcilinea* (Bösenberg and Strand, 1906); *P. debilis* (Thorell, 1891); *P. suavis* (Simon, 1885); *P. vittata* (Koch, 1846) (Żabka 1985; Peng & Li 2003; Ono et al. 2012; Logunov & Jäger 2015; Luong et al. 2016; Logunov 2021).

In this study, a new jumping spider species *Phintella daklak* Hoang sp. nov. (♂♀) discovered in the Chu Yang Sin National Park, Dak Lak Province, Vietnam is described. Furthermore, the species *P. sancha* Cao & Li, 2016 based on a male specimen from Buon Ma Thuot City, also in Dak Lak Province, Vietnam is documented, herein. In all, nine species of the genus *Phintella* are recorded in Vietnam.

MATERIAL AND METHODS

All specimens used in the present study were collected by beating sheet. The specimens were examined using a Leica M205C stereo microscope. Photos were captured using a Jenoptik ProgRess CF Scan 12.5MP camera and Jenoptik ProgRes Capture Pro ver. 2.10.0.1 software. The male palp and female epigyne were dissected and examined, and the female genitalia were cleared in a 10% KOH solution at room temperature for approximately 12 hours. Photos were stacked using Helicon Focus ver. 8.2.2 Pro software and then edited using Adobe Photoshop CS2 ver. 9.0. All measurements are given in millimeters (mm). The terminology of leg spination follows Ono (1988). Measurements of leg segment lengths are presented as follows: femur + patella + tibia + metatarsus + tarsus (total length). The studied specimens have been deposited at the Vietnam National Museum of Nature (VNMN) in Hanoi, Vietnam.

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Abbreviations used in the article

ALE = anterior lateral eye
AME = anterior median eye
PLE = posterior lateral eye
PME = posterior median eye
Fm = femur
Pt = patella
RTA = retrolateral tibial apophysis
Tb = tibia
Mt = metatarsus

Abbreviations for morphological terms (position of spines on legs)

ap = apical
d = dorsal
pr = prolateral
rt = retrolateral
v = ventral

RESULTS

Taxonomy

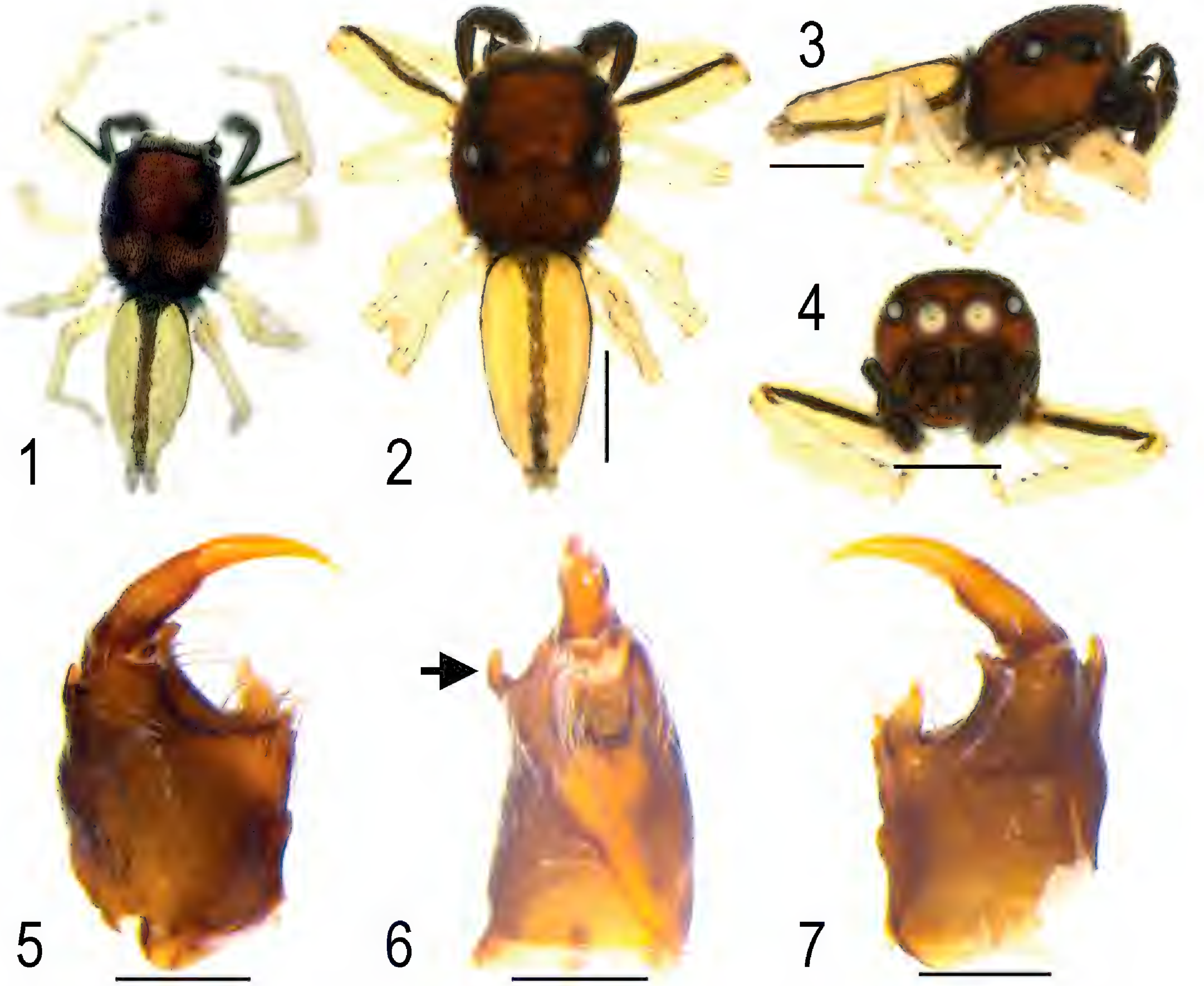
Family **Salticidae** Blackwall, 1841
Genus ***Phintella*** Strand, 1906

Phintella daklak Hoang sp. nov.
urn:lsid:zoobank.org:act:7AAF7DA8-33F0-4AA0-8CD0-F75EA9DF3ECA
Figs 1–20

Type material

Holotype

VIETNAM • ♂ (VNMN-ARA-SAL-71.1); Dak Lak Prov., Krong Bong District, Chu Yang Sin National Park; 12.42405° N, 108.3476° E; 608 m a.s.l.; 15 Feb. 2022, Q.D. Hoang leg.



Figs 1–7. *Phintella daklak* Hoang sp. nov., ♂ (VNMN-ARA-SAL-71.1). 1. Habitus (in life), dorsal view, without scale. 2. Same (in ethanol), dorsal view. 3. Same, lateral view. 4. Carapace, frontal view. 5. Left chelicera, frontal view. 6. Same, with a dorsal hook (black arrow), lateral view. 7. Same, posterior view. Scale bars: 2– 4 = 1 mm; 5–7 = 0.3 mm.

Paratypes

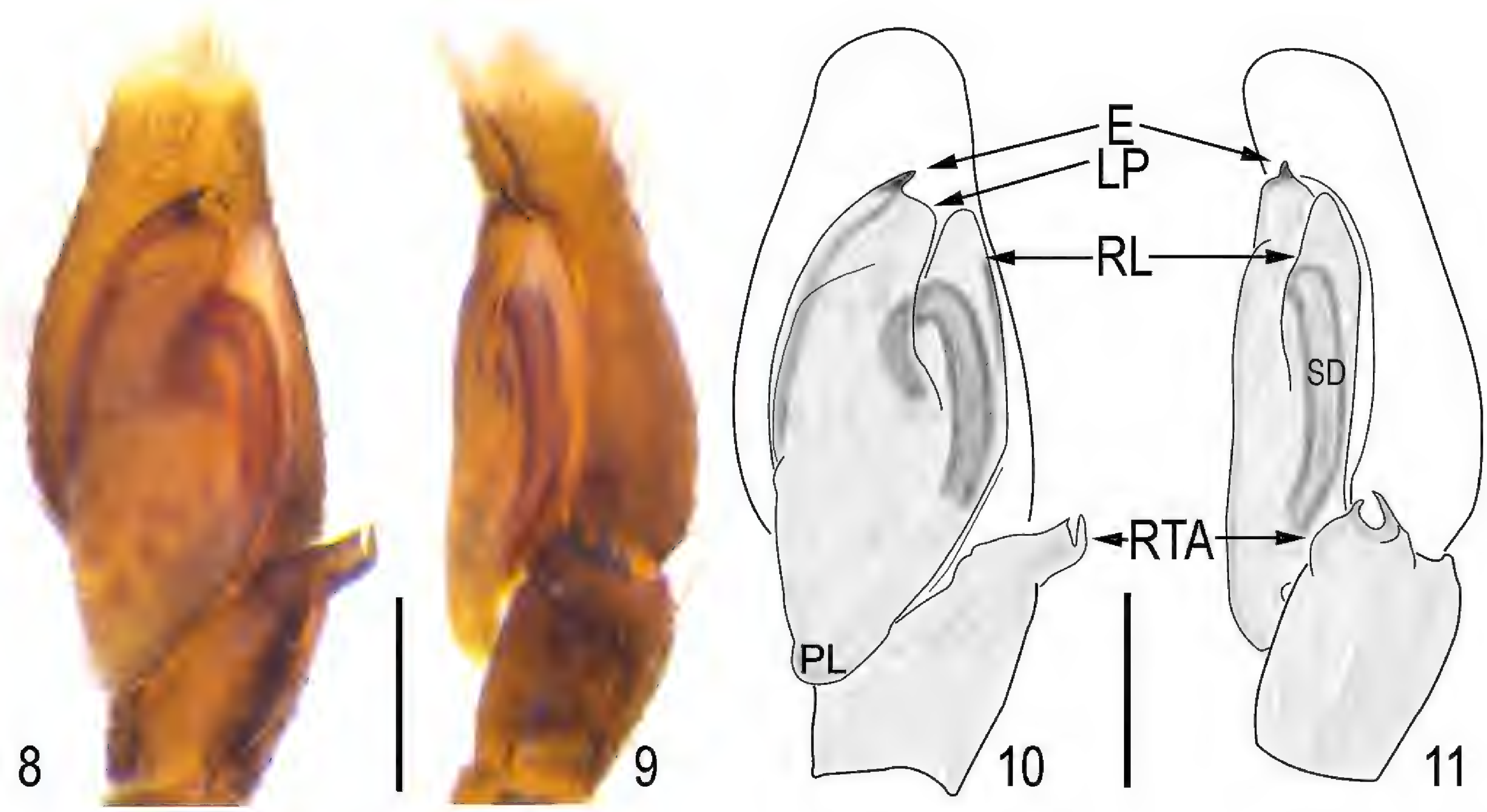
VIETNAM • 6 ♀♀ (VNMN-ARA-SAL-38.1-7), 1 ♂ (VNMN-ARA-SAL-71.2); same collection data as for holotype • 1 ♀ (VNMN-ARA-SAL-51), 1♂ (VNMN-ARA-SAL-71.3); Dak Lak Prov., Buon Ma Thuot City; 12.5971° N, 108.0528° E; 392 m a.s.l.; 19 Feb. 2022; Q.D. Hoang leg.

Etymology. This specific epithet is derived from the type locality, Dak Lak Province, where the species was found; noun in apposition.

Diagnosis. The male of the new species *Phintella daklak* Hoang sp. nov. resembles *P. suavisoides* Lei & Peng, 2013 in having male with short embolus (Figs 8–11), bulbus without tegulum bump, presence of retrolateral lobe of tegulum, posterior lobe directed prolaterad (Figs 8, 10), and bifurcated RTA (Figs 8–11), but differs from *P. suavisoides* in having embolus short and directed at 2 o'clock position (longer and directed at 1 o'clock in *P. suavisoides*, Lei & Peng 2013: fig. 6a; Cao et al. 2016: fig. 36c–d), retrolateral lobe of tegulum relatively longer in the new species (Figs 8–11) compared to *P. suavisoides* (Lei & Peng 2013: fig. 6a–b; Cao et al. 2016: fig. 36b–d), posterior lobe directed at 8 o'clock (Figs 8, 10) vs. 6:30 o'clock in *P. suavisoides* (Lei & Peng 2013: fig. 6a; Cao et al. 2016: fig. 36c–d), tibia almost half as long as cymbium (about a third in *P. suavisoides),* RTA elongated and slanted, longer than of that of *P. suavisoides* (Lei & Peng 2013: fig. 6a–c; Cao et al. 2016: fig. 36b–c). Female of the new species is most similar to those of *P. mii*, *P. banna* and *P. suavisoides* (see comparative illustrations in Metzner 2023), but can be distinguished by the following characters: epigyne with two pockets (Figs 16–17, 19), copulatory opening far from each other, copulatory ducts almost straight, aligned in V-shape, and relatively narrow, and spermathecae touching each other.

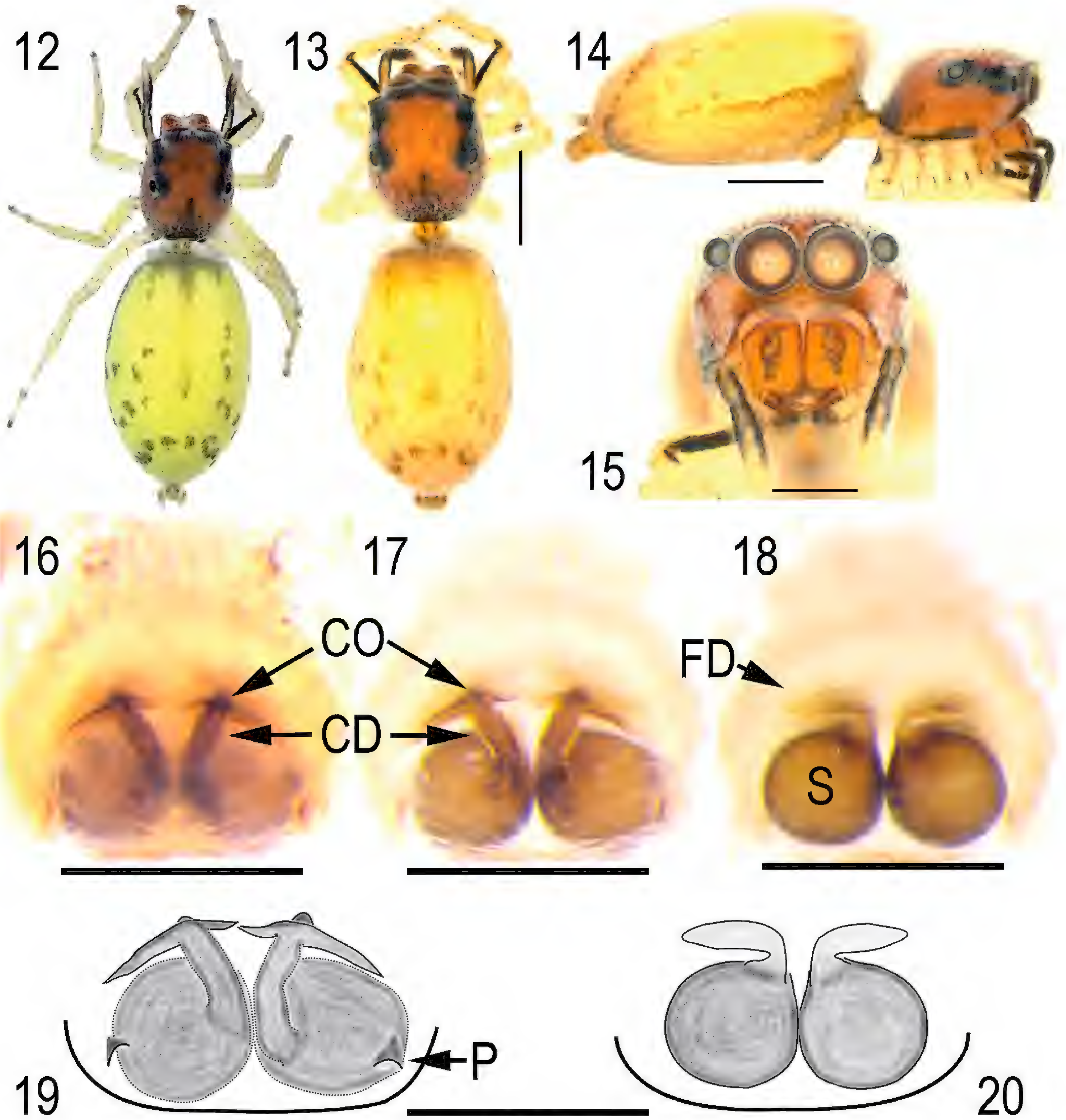
Description

Male (holotype). Measurements: Carapace length 1.78, width 1.51; Abdomen length 2.01, width 0.99. Clypeus height 0.03. Carapace reddish brown, clothed with dense black hairs (Figs 1–4), some protruding long pale hairs. Anterior eyes surrounded by yellow-orange orbital setae (Fig. 4), continuous dark patch from ALE to PLE. Clypeus dark brown (Fig. 4), three stout and long pale setae located above clypeus medially. Sternum yellowish. Endites and labium yellowish brown, with light yellow tip. Chelicerae dark brown with a hook dorsally (Figs 5–7); promargin with one tooth, two larger retromarginal teeth (Figs 5–7). Abdomen yellowish, with a same sized dark longitudinal band of dorsum with a little broadens anteriorly (Figs 1–2). Lateral sides of the abdomen with a dark longitudinal band (Fig. 3), lateral and dorsal bands united anteriorly. Spinnerets yellowish covered with spare dark hairs. Leg pale yellow (except femora with dark band prolaterally). Width of eye rows: anterior eye row 1.29; posterior medial eye row 1.14; posterior lateral eye row 1.30. Distance between ALE-PME 0.40; ALE-



Figs 8–11. *Phintella daklak* Hoang sp. nov., ♂ (VNMN-ARA-SAL-71.1). 8. Left palp, ventral view. 9. Same, retrolateral view. 10. Same, ventral view. 11. Same, retrolateral view. Scale bars: 8–11 = 0.2 mm. Abbreviations: E = embolus; LP = lamellar process; PL = posterior lobe; RL = retrolateral lobe of tegulum; RTA = retrolateral tibial apophysis; SD = sperm duct.

PLE 0.84. Diameter of eyes: AME 0.45; ALE 0.21; PME 0.04; PLE 0.20. Length of leg segments: I 1.27 + 0.69 + 0.88 + 0.75 + 0.32 (3.91); II 0.90 + 0.47 + 0.54 + 0.58 + 0.31 (2.80); III 1.13 + 0.48 + 0.75 + 0.87 + 0.33 (3.56); IV 1.21 + 0.42 + 0.86 + 1.02 + 0.38 (3.89). Leg formula IV–I–III–II. Leg spination: I: Fm d 1–1–1; Ti v 2–2–2; Mt v 2–2ap. II: Fm d 1–1–3; Tb v 2–2; Mt v 2–2ap. III: Fm d 1–1–3; Tb pr 0–0–1, rt 0–0–1, v 0–1–0; Mt d 0–0–2, rt 1–0–1, v 0–1–2 and IV: Fm d 1–1–3; Tb pr 0–0–1, rt 0–1–1, v 0–0–1ap; Mt d 0–0–2, rt 1–1–1, v 0–1–2.



Figs 12–20. *Phintella daklak* Hoang sp. nov., ♀ (VNMN-ARA-SAL-38.1). 12. Habitus (in life), dorsal view, without scale. 13. Same (in ethanol), dorsal view. 14. Same, lateral view. 15. Carapace, frontal view. 16. Epigyne (unmacerated), ventral view. 17. Epigyne (cleared in KOH), ventral view. 18. Vulva, dorsal view. 19. Epigyne, ventral view. 20. Vulva, dorsal view. Scale bars: 13–14 = 1 mm; 15 = 0.5 mm; 16– 20 = 0.2 mm. Abbreviations: CD = copulatory duct; CO = copulatory opening; FD = fertilization duct; P = pocket; S = spermathecae.

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Palp (Figs 8–11) dark brown; tibia nearly half as long as cymbium (Figs 8–11); RTA elongated, slanted, and bifurcated, wrench-like (Figs 8–11). Posterior lobe directed prolaterally (Figs 8, 10). Embolus short, pointed, strongly sclerotized, directed at two o'clock (Figs 8–11). Lamellar process triangular (Figs 8, 10). Retrolateral lobe of tegulum long, trapezoid in ventral view (Figs 8, 10).

Female. Measurements: Carapace length 1.51, width 1.28; Abdomen length 2.85, width 1.75. Clypeus height 0.03. Carapace orange, clothed with dense white hairs (Figs 12–15), with some protruding long pale hairs. Anterior eyes surrounded by white orbital setae (Fig. 15), continuous dark patch from ALEs to PLEs. Clypeus brown (Fig. 15), three stout and long pale setae located above clypeus medially. Sternum yellowish with dark brown rim. Endites and labium yellowish. Chelicerae yellowish with dark patch, without a hook, promargin with two teeth, and one retromarginal tooth. Abdomen yellowish, with scatter of small black hair spots on dorsum (Figs 12–13). Lateral sides of abdomen darker (Fig. 14). Spinnerets yellowish covered with spare dark hairs. Legs pale yellow (except femora with dark prolateral band). Width of eye rows: anterior eye row 1.14; posterior medial eye row 1.05; posterior lateral eye row 1.17. Distance between ALE-PME 0.37; ALE-PLE 0.76. Diameter of eyes: AME 0.39; ALE 0.18; PME 0.03; PLE 0.18. Length of leg segments: I 0.76 + 0.39 + 0.51 + 0.46 + 0.26 (2.38); II 0.71 + 0.34 + 0.44 + 0.41 + 0.23 (2.13); III 0.88 + 0.35 + 0.56 + 0.67 + 0.24 (2.70); IV 1.04 + 0.74 + 0.75 + 0.83 + 0.31 (3.67). Leg formula IV–I–III–II. Leg spination: I: Fm d 1–1–1; Ti v 2–2–2; Mt v 2–2ap. II: Fm d 1–1–3; Tb v 2–2; Mt v 2–2ap. III: Fm d 1–1–3; Tb pr 0–0–1, rt 0–1–1; Mt d 0–1–2, rt 1–0–1, v 0–0–2 and IV: Fm d 1–1–3; Tb pr 0–0–1, rt 0–1–1, v 0–0–1ap; Mt d 0–1–2, pr and rt 0–0–1, v 0–0–2.

Epigyne (Figs 16–20) with two small pockets, copulatory openings complemented by an anterior rim as hammerhead-like (Figs 16–17, 19), copulatory ducts narrow, almost straight, converging posteriorly (V-shaped) in ventral view (Figs 16–17, 19), copulatory ducts connected to inner mid portion of spermathecae (Figs 16–17, 19); spermathecae large, spherical, touching each other (Figs 17–20).

Distribution. Known only from the type locality.

Phintella sancha Cao & Li, 2016
Figs 21–23
Phintella sancha Cao & Li, in Cao, Li & Żabka 2016: 91, figs 34a–d, 35a–b (Dm).

Material examined

VIETNAM • 1 ♂ (VNMN-ARA-SAL-72); Dak Lak Prov., Buon Ma Thuot City; 12.5971° N, 108.0528° E; 392 m a.s.l.; 19 Feb. 2022; Q.D. Hoang leg.

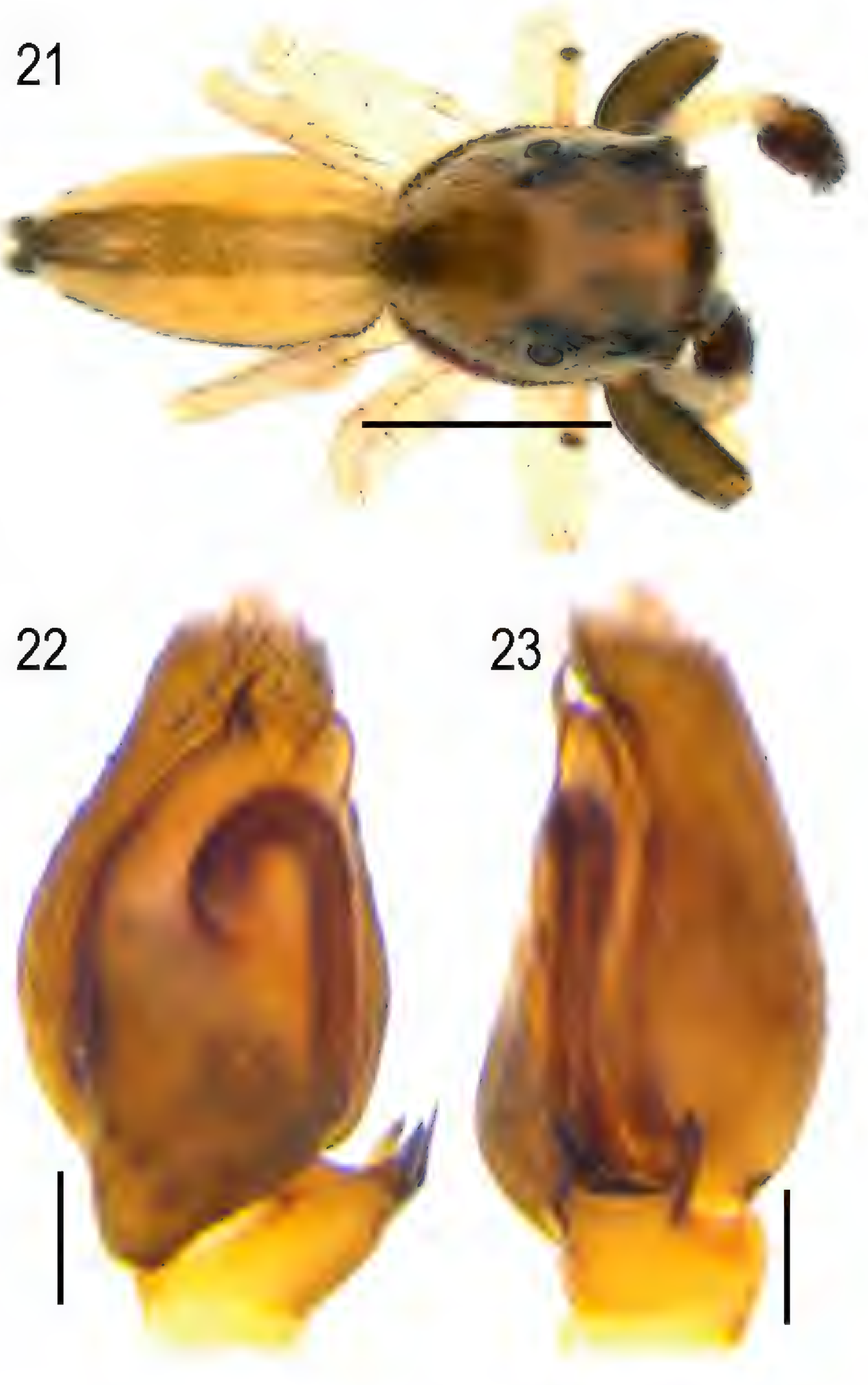
Diagnosis. The species *Phintella sancha* is closely related to the new species, *P. daklak* sp. nov. and *P. suavisoides* in palpal structure and general appearance. However, it differs from both latter species by embolus thin, longer, claw-shaped (Figs 22–23) (thicker and shorter in *P. daklak* and *P. suavisoides*); tibia wider than long (longer than wide in *P. daklak* and *P. suavisoides*), RTA with three branches (Figs 22–23) vs. two in both *P. daklak* and *P. suavisoides*.

Description. See Cao et al. 2016. Habitus and male palp from Vietnam as in Figs 21–23.

Distribution. China (Yunnan Prov.) and Vietnam (Dak Lak Prov.).

DISCUSSION

With the addition of a new species and a new record from the Central Highlands, the genus *Phintella* Strand, 1906 in Vietnam now comprises nine species. Vietnam is divided into three distinct regions: north (which includes northwestern, northeast and Red River Delta areas), cen-



Figs 21–23. *Phintella sancha* Cao & Li, 2016, ♂. 21. Habitus, dorsal view. 22. Left palp, ventral view. 23. Same, retrolateral view. Scale bars: 21 = 1 mm; 22–23 = 0.1 mm.

tral (north central coast, south central coast and central highlands) and south (southeastern and Mekong River Delta areas). The distribution of the genus in Vietnam exhibits a decreasing trend in the number of species from north to south. For instance, three species, namely, *P. accentifera, P. debilis* and *P. suavis* are restricted to northern Vietnam (Żabka 1985; Peng & Li 2003), the species *Phintella aequipeiformis* is distributed from north to central Vietnam (Żabka 1985; Luong et al. 2016), the species *P. daklak* Hoang sp. nov., *P. sancha* and *P. argenteola* are exclusively found in central Vietnam while the species *P. vittata* and *P. bifurcilinea* are distributed throughout the country (Żabka 1985; Peng & Li 2003; Logunov & Jäger 2015; Logunov 2021).

Although the western neighboring countries of Vietnam, Laos and Cambodia, have not recorded any representatives of the genus *Phintella*, China in the north has recorded the largest number of species of this genus, with more than 30 species (Metzner 2023). Therefore, it is expected that more *Phintella* species will be found in Vietnam, especially in the north.

However, to accurately determine the true diversity of this genus, as well as the salticid fauna in Vietnam, more extensive surveys are required to cover all regions of the country.

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Research article

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A new genus and species, *Brixiola perinetana* gen. et sp. nov., of planthoppers (Hemiptera: Fulgoromorpha: Cixiidae) from Madagascar

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Abstract. A new genus from Madagascar, *Brixiola* Walczak, Gębicki & Taszakowski gen. nov., with its type species *Brixiola perinetana* Walczak, Gębicki & Taszakowski sp. nov. are described and placed in the tribe Brixiini (Hemiptera: Fulgoromorpha: Cixiidae). In its external structure, the new taxon is most similar to species of the genus *Brixia* Stål. Photographs of the adult, illustrations of male genitalia and SEM micrographs of the morphological characters of new species are also provided.

Key words. new genus, new species, planthoppers, Brixiini, taxonomy, Madagascar.

INTRODUCTION

The planthopper family Cixiidae Spinola, 1839 (Hemiptera: Fulgoromorpha) comprises 16 extant tribes (Spinola 1839; Holzinger et al. 2002; Szwedo 2004; Bourgoin 2023). Four of them (i.e., Andini Emeljanov, 2002, Brixidiini Emeljanov, 2002, Brixiini Emeljanov, 2002, and Bennini Metcalf, 1938) probably form a genetically close and morphologically similar group (Metcalf 1938; Emeljanov 2002; Ceotto et al. 2008). These tribes, except for the Brixiini, comprise only a few genera and species characterized by forewings held steeply tectiform in repose.

The tribe Brixiini comprises nine genera inhabiting the southern part of the Eastern Hemisphere. The type genus *Brixia* Stål, 1856, which is the largest genus in the Brixiini comprising about 120 species (Stål 1856; Emeljanov 2002), has the broadest range, including the Oriental and Afrotropical regions (Bourgoin 2023) and also the Australasian region, with two known species from Papua New Guinea (Walker 1870). The other genera, with fewer species, show a significant degree of endemism. The richest region in terms of the number of endemics is the Australasian region with the genera *Innobindus* Jacobi, 1928 (seven species), *Solonaima* Kirkaldy, 1906 (15 species), *Undarana* Hoch & Howarth, 1989 (six species), and *Ithma* Fennah, 1969 (three species) (Kirkaldy 1906; Jacobi 1928; Fennah 1969; Hoch & Howarth 1989; Erbe & Hoch 2004; Löcker et al. 2007). A single genus, *Melandeva* Distant, 1906, with two species is known from the Oriental region (Distant 1906; Emeljanov 2007) and there are three genera in the Afrotropical region, namely *Caffrocixius* Fennah, 1967 (six species), *Cibrica* Emeljanov, 2007 (four species), and the monotypic genus *Typhlobrixia* Synave, 1953 (Synave 1952, 1953, 1969; Paulian 1953; Fennah 1967; Van Stalle 1984, 1987; Emeljanov 2007; Soulier-Perkins et al. 2015).

Adults of the tribe Brixiini feed on various plant species, but they are probably not restricted to a specific host plant. Nymphs live underground and feed on the underground parts of plants, like most species of the Cixiidae family; a fact that may explain the tendency to form numerous cavernicolous species (about 30 within the family Cixiidae). These troglobionts feed on the roots of epigeic plants in the subterranean zone of tropical caves, which were formed mainly in sedimentary rocks, and include *Typhlobrixia namorokensis* Synave, 1953 from Madagascar, *Brixia briali* Hoch & Bonfils, 2003 from Réunion,

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plus six species of the genus *Solonaima* and two species of *Undarana*, which are Australasian endemics (Kirkaldy 1906; Synave 1953; Hoch & Howarth 1989; Hoch et al. 2003; Löcker et al. 2007).

In Madagascar there are 40 Brixiini taxa: 39 representatives of the genus *Brixia* described so far (Signoret 1860; Jacobi 1917; Lallemand & Synave 1954; Synave 1956, 1965, 1979; Bourgoin 2023) and one endemic troglobiont *Typhlobrixia namorokensis* (Synave 1952, 1953; Paulian 1953; Soulier-Perkins et al. 2015). Species of the genus *Brixia* known from Madagascar constitute a large group, but the information about them is fragmentary. The majority of species were reported from the northeastern areas and the eastern coast of the island, also including the areas near the capital city, Antananarivo. Almost all Madagascan species of the genus *Brixia* are endemics (Signoret 1860; Stål 1866; Jacobi 1917; Lallemand & Synave 1954; Synave 1956, 1965, 1979), except for *Brixia krameri* Synave, 1979, which also occurs in Seychelles (Holzinger et al. 2008). *Brixia* species are usually medium-sized, which in Madagascar reach sizes between 5–10 mm in length, and contrastingly coloured. Adult *Brixia* specimens are usually observed from September to March (Lallemand & Synave 1954; Synave 1956, 1965). Information about host plants of *Brixia* species found in Madagascar is lacking. The representatives of this genus that occur in nearby Mascarene islands feed on a wide range of plant species belonging to at least 17 genera of 14 families of Magnoliophyta (Williams 1975; Bonfils et al. 1994; Attié et al. 2002, 2005, 2008). Thus, it can be assumed that the trophic preferences of the species of *Brixia* from Madagascar may be similar to those from Mascarene islands.

Here we described a new cixiid taxa, *Brixiola perinetana* gen. et sp. nov. from Madagascar based on a male collected in Perinet. We owe the description of this new genus and species to Henri Synave (1921–1980) – a Belgian entomologist who described 55 species of the genus *Brixia* Stål, which is closely related to the genus *Brixiola* gen. nov., and over 300 other planthopper species and 25 genera. The label attached by Synave drew our attention and directly helped us to prepare the present study. Synave considered the specimen to belong to the genus *Brixia*.

MATERIALS AND METHODS

Morphological features of the specimen were imaged using a Leica M205C stereo microscope with a Leica LED5000 HDI (high diffuse dome illuminator), a Leica DFC495 digital camera, and the Leica application suite ver. 4.9.0 software. SEM pictures were obtained using Phenom XL field emission scanning electron microscope with a Back-Scatter Detector (BSD). The panoramic image stitcher Image Composite Editor ver. 3.0 and graphic editor Adobe® Photoshop CS6 were used to prepare the figures. The specimen was only cleaned with a brush because other methods, e.g., washing or dehydration, may damage the individual. Next, the specimen was mounted on aluminium stubs (an insect pin was inserted into a piece of the sponge glued to the stub). In the next stage, the specimen was covered with an anti-static spray. The measurements were taken with the Leica application suite ver. 4.9.0 software. The abdomen was boiled three times (about 10 minutes) in a 10% solution of potassium hydroxide (KOH) according to Knight's method (Knight 1965). The genitalia were detached from the abdomen after boiling. The specific parts of the genital structures were separated from the abdomen using thin forceps and a needle blade. Next, these structures were placed in glycerine. The genitalia were studied and drawn with the Nikon Ni-U light microscope with a camera lucida.

The morphological terminology of the head, thorax and legs follows Holzinger et al. (2003) and Ceotto & Bourgoin (2008), for male genitalia it follows Bourgoin (1987), and the terminology of venation of fore- and hindwings follows Anufriev & Emeljanov (1988) and Bourgoin et al. (2015). The terminology and classification of sensilla follow Bourgoin & Deiss (1994), Holzinger et al. (2002), Romani et al. (2009), and Wang et al. (2018).

In the description of the type labels, the contents of each label are enclosed within double quotation marks (“ ”), the individual lines of data are separated by a double forward slash (//), and the author's comments are between square brackets ([]).

RESULTS

Brixiola Walczak, Gębicki & Taszakowski gen. nov.

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(Figs 1–4)

Type species: *Brixiola perinetana* Walczak, Gębicki & Taszakowski gen. et sp. nov.

Diagnosis

Apical part of the head elongated and very narrow, its width slightly smaller than width of compound eye. Frons widest much above the median ocellus and considerably tapering towards the frontoclypeal suture. Lateral carinae in the apical part of the head located very close to each other, but not fused. Narrower (apical) part of the frons concave, delimited by two transverse carinae in the upper apical area of the head. Antenna base located above posterior margin of compound eyes. Semicircular scapus four times shorter than cylindrical pedicellus. Median ocellus located at the distance slightly greater than its diameter from the arcuated frontoclypeal suture. Lateral margins of frons and clypeus clearly intended in the area of frontoclypeal suture (these margins do not form one uniform arcuate line). Outer edge of metatibia with a row of small spines. Apex of metatibia with a rim of spines including two long lateral and two short middle spines. Apex of metatarsomere I with one long and three short spines; apex of metatarsomere II with one long and two short spines. The basal concavity of costal margin of tegmen absent. In forewings, ScP considerably delimited the posterior margin of lanceolate pterostigma. Length of common stem of ScP+R+M almost equal to the length of basal cell. Vein R separating in a total of seven branches: RA branches into RA_1 and RA_2 and RP branches into $RP_1 – RP_5$. There are five MP branches, initially fused in a common stem MP, which forks into MP_{1+2}, MP_3 and MP_{4+5} branches. CuA_1 arched opposite to MP_{4+5}. In the hindwings r-m connected with M at the point where MP separating from M. The length of the common vein Cu almost equal to the length of basal cell (bc). The section of the inner edge located between the apex of clavus and the end of oblique vein icu strongly shortened. Slender periandrium with broad basal crest-like appendage and four long apical spines. Flagellum in the ventral view with a short apical spine and a row of small spines and in the lateral view with three broad short teeth and long basal spine. Apex of parameres pallete-shaped extended. Apical lobes of anal tube narrow and curved downwards.

Description

Head. Head including eyes narrower than pronotum. Vertex trapezoidal, approximately two times wider than long, deeply indented in the middle, lateral carinae merged and connected by short arcuate carina. At apex of vertex short groove. Width of basal part of vertex slightly smaller than width of compound eye (in dorsal view) (Fig. 1B). Frons strongly expanded, its lower part distinctly wider than compound eye, oval-shaped. Lateral carinae weakly concave. Apical part of head marginated with two short transverse and separated carinae. Transverse subapical carina interrupted in the middle and strongly arched. Apical carina (separating frons from vertex) oblique. These carinae delimited a small area of irregular shape located in the apical part of the head between vertex and frons. Frontoclypeal suture weakly visible, concave, arched, its convexity directed towards median ocellus. Postclypeus slightly shorter than frons. Anteclypeus at least three times shorter than postclypeus. Both with distinct median carina, reaching about half of the length of postclypeus. Lateral margins of frons and clypeus (in lateral view) considerably intended in the area of frontoclypeal suture (they do not form one uniform arcuate line). Rostrum long, its tip exceeds the line between coxae III (hind coxae) (Figs 1A, 2A). Median

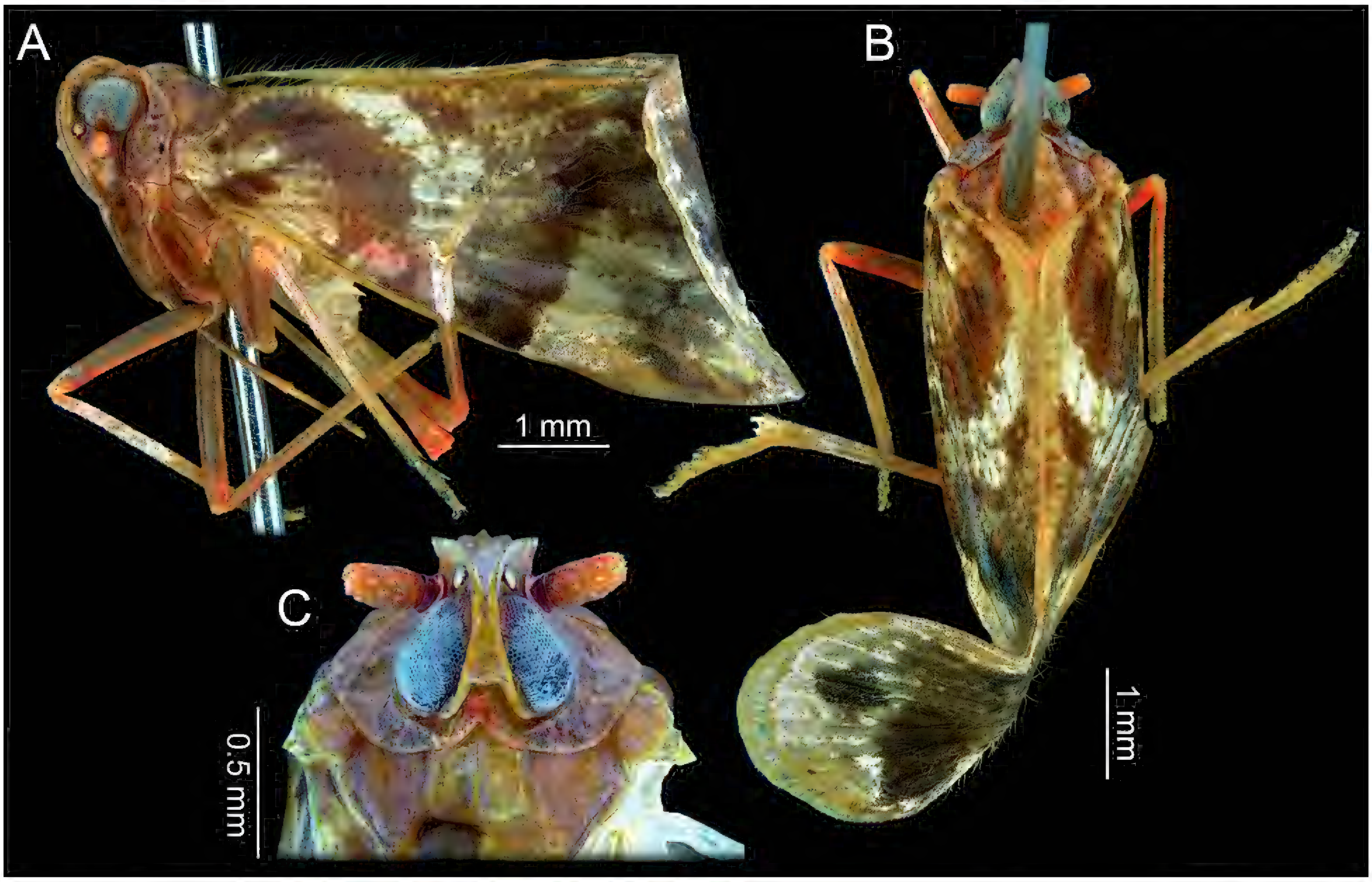

Fig. 1. *Brixiola perinetana* gen. et sp. nov., Walczak, Gębicki & Taszakowski. **A**. Habitus, lateral view. **B**. Habitus, dorsal view. **C**. Vertex and pronotum, dorso-anterior view.

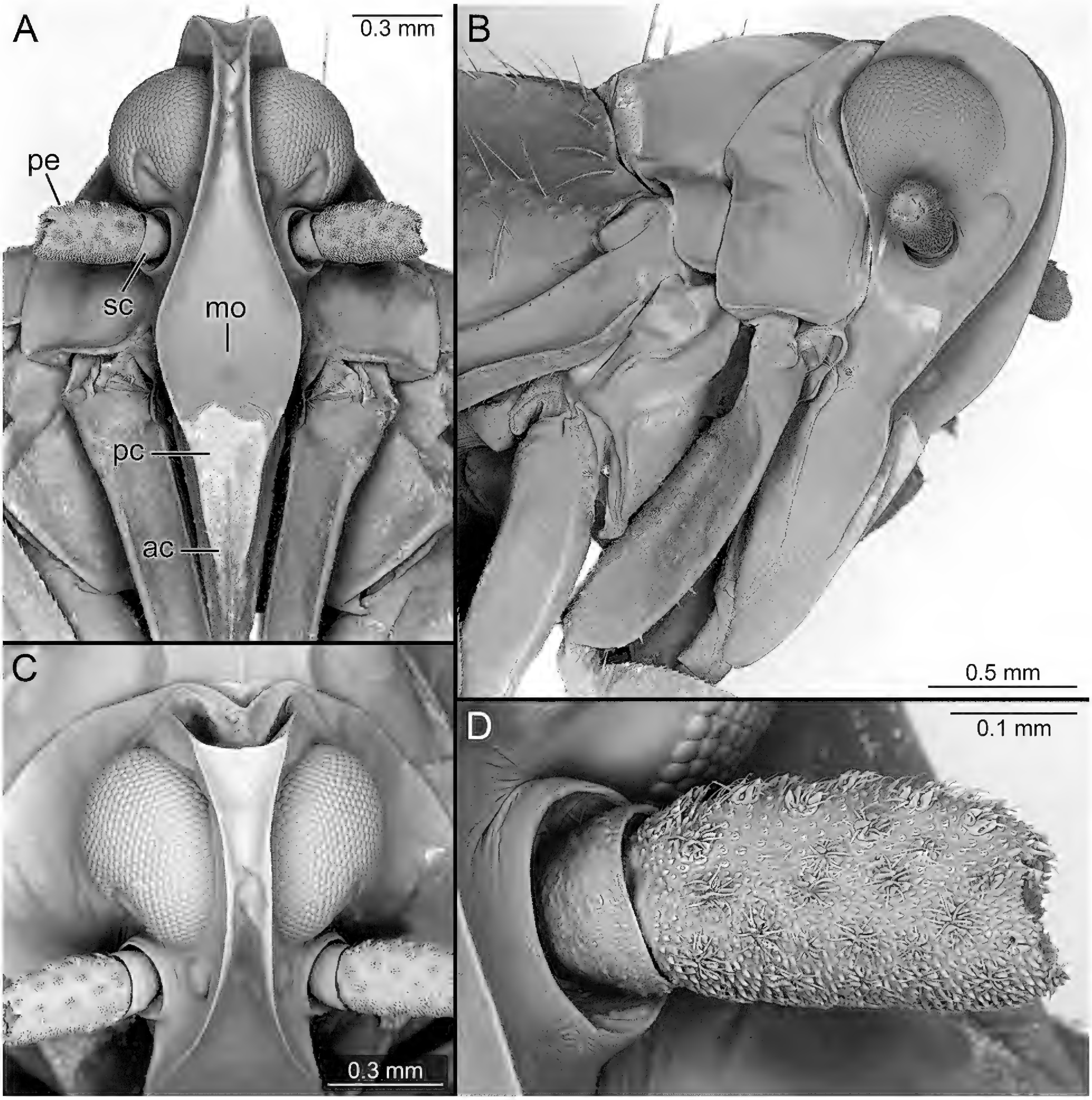

Fig. 2. *Brixiola perinetana* gen. et sp. nov., Walczak, Gębicki & Taszakowski, SEM detail of morphology. **A**. Head, frontal view. **B**. Head, lateral view. **C**. Vertex and pronotum, anterodorsal view. **D**. Antenna, lateral view. Abbreviations: ac = anteclypeus; mo = median ocelli; pc = postclypeus; pe = pedicellus; sc = scapus.

ocellus distinct, located at the distance slightly greater than its diameter from the arcuated frontoclypeal suture. Lateral carina regularly rounded (Fig. 2A). Above ocelli, near margin of the compound eye, two sockets of sensory organs (Fig. 3C). On gena above the arcuate genal groove, near the hind margin of head, sensory organ with complex structure (Fig. 3B). Cylindrical pedicellus four times longer than semicircular scapus, about twice longer than wide. Antennae embedded in deep cavities highly fringed with cuticular collar (Fig. 2D). Surface of pedicellus (beside narrow basal part) covered with sensory plate organs (Figs 2D, 3A). Centrally located, slightly convex sensory plate covered on the inner side with single ones, and on outside most often by long, curved and tapered processes clustered in pairs. The ventral side of pedicellus covered densely with cuticular processes (also occurring within plate organs). Single sensilla trichoidea (short and straight) are scattered between them. Dorsal side of pedicellus with cuticular microtubercles (much larger than on ventral side) almost exclusively within sensory plate organs. Between plate organs, numerous sensilla trichoidea (long and curved) (Fig. 2D).

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Table 1. Comparison of the *Brixiola* gen. nov. and the genus *Brixia.*

Feature	*Brixiola* gen. nov.	*Brixia*
apical part of the frons (Figs 2A–C)	elongate and concave; median suture absent	flat; short median suture present
basal concavity of forewing costal margin (Fig. 3F)	absent	present
RP veins on forewing (Fig. 3F)	five RP veins, RP_3 and RP_4 connected in the basal part	three to five RP veins, the last two connected in the basal part
apex of metatibia	with seven spines, including two lateral, longest and two median, shortest spines	with six spines, the outer longest, and two median, the shortest spines
periandrium (Figs 4A–B)	with a large ventral crest without spines	without the ventral crest or with ventral crest with spines
flagellum (Figs 4A–B)	with an elongated spine, row of small spines, three short lateral teeth and one apical teeth	only with long spines
apical lobes of anal segment (Figs 4E–F)	narrow and curved downwards	broad and not curved downwards

Thorax. Pronotum very short, with broad paranotal lobes and posterior margin intended in right angles (Figs 1B–C, 2C). Mesonotum with three longitudinal carinae including median carina reaching the base of scutellum (Fig. 1C).

Legs. Fore legs: procoxa elongated, about three times longer than wide, slightly concave on ventral site, with long, arcuate groove. Profemur 1.6 times longer than procoxa, slightly concave on the lateral side, the inner side with median ridge armoured with small denticles. Lower margin with very small spines. Protibia about 1.4 times longer than profemur (Fig. 1A). Middle legs: mesocoxa elongated and widest in basal part with a straight groove on the lateral side. Mesofemur short about 1.4 times shorter than coxa. Mesotibia rectangular in cross-section, about three times longer than mesofemur with margins densely covered with small spines. Second tarsomere shortest. Hind legs: metacoxa robust with spines. Outer margin of metatibia with a row of small spines. Apex of metatibia with a rim of seven spines including two long lateral spines (the inner spine is slightly shorter than outer one), three short median spines connected to each other and two medium-sized spines on inner surface of apex of tibia. The apex of metatarsomere I with one long and three short spines; apex of metatarsomere II with one long and two short spines. All tarsomeres equal in length (Fig. 1A).

Wings. Forewing strongly expanded in the anterior part. Basal and middle band reaching the costal margin of clavus where they are widest. The basal concavity of costal margin of tegmen absent. The common stem of ScP+R+M almost as long as basal cell. RA forks into RA_1 and RA_2. Long stem RP forks behind pterostigma into single RP_1, RP_2, bifurcated RP_{3+4} and RP_5. MP forks into MP_1 and MP_2, although short stem MP_{3+4+5} forks into single MP_3 and forked MP_4 and MP_5 (according to the venation pattern: $MP_{1+2,}$ MP_3 and MP_{4+5}). CuA distinctly bent doubly arched. The length of oblique vein icu not greater than that of transverse veins. Forking of CuA_2 and icu located slightly above the apex of clavus. The section of inner edge between apex of clavus and end of oblique vein icu strongly shortened. Most apical cells are the same size and shape and slightly longer than corresponding subapical cells (Figs 3D–E). Hind wing. Costal margin of hind wings slightly arched. Nodus elongated and narrow, located approximately in the middle of the wing length. Forkss of RP_1 and RP_2 reaching the anterior margin of nodus (before the apex of nodus). Relatively long vein r-m connected with M at the point where MP separating from M. Common stem of MP and CuA_1 elongated and slightly shorter than r-m. The length of the common vein Cu (at the base of the wing) almost equal to the length of basal cell (bc) (Figs 3F–G).

Male genital structure. Aedeagus relatively long and narrow with roundish ventral crest (Fig. 4A). The dorsal edge of periandrium almost straight (without crest), basal lobe directly connected with the anal segment (Fig. 4F). In frontal part of periandrium, a pair of elongated spines with combined bases. First one long, reaching the base of periandrium, second one bent backward in the middle of its length. On both sides of the apical part of the periandrium, one single straight spine (Figs 4A–B). Flagellum in the ventral view with a short apical spine and a row of small spines and in the lateral view with three broad short teeth and long basal spine. Parameres with long stems and obliquely placed apical lobes (Fig. 4C). Anal segment with large anal style. Apical lobes of anal tube narrow and curved downwards (Figs 4D–E).

Remarks. In its external structure, including the male genitalia, *Brixiola* gen. nov. is similar to many representatives of the tribe Brixiini and even Brixidiini. *Brixiola* gen. nov. is distinguished by elongated, laterally flattened

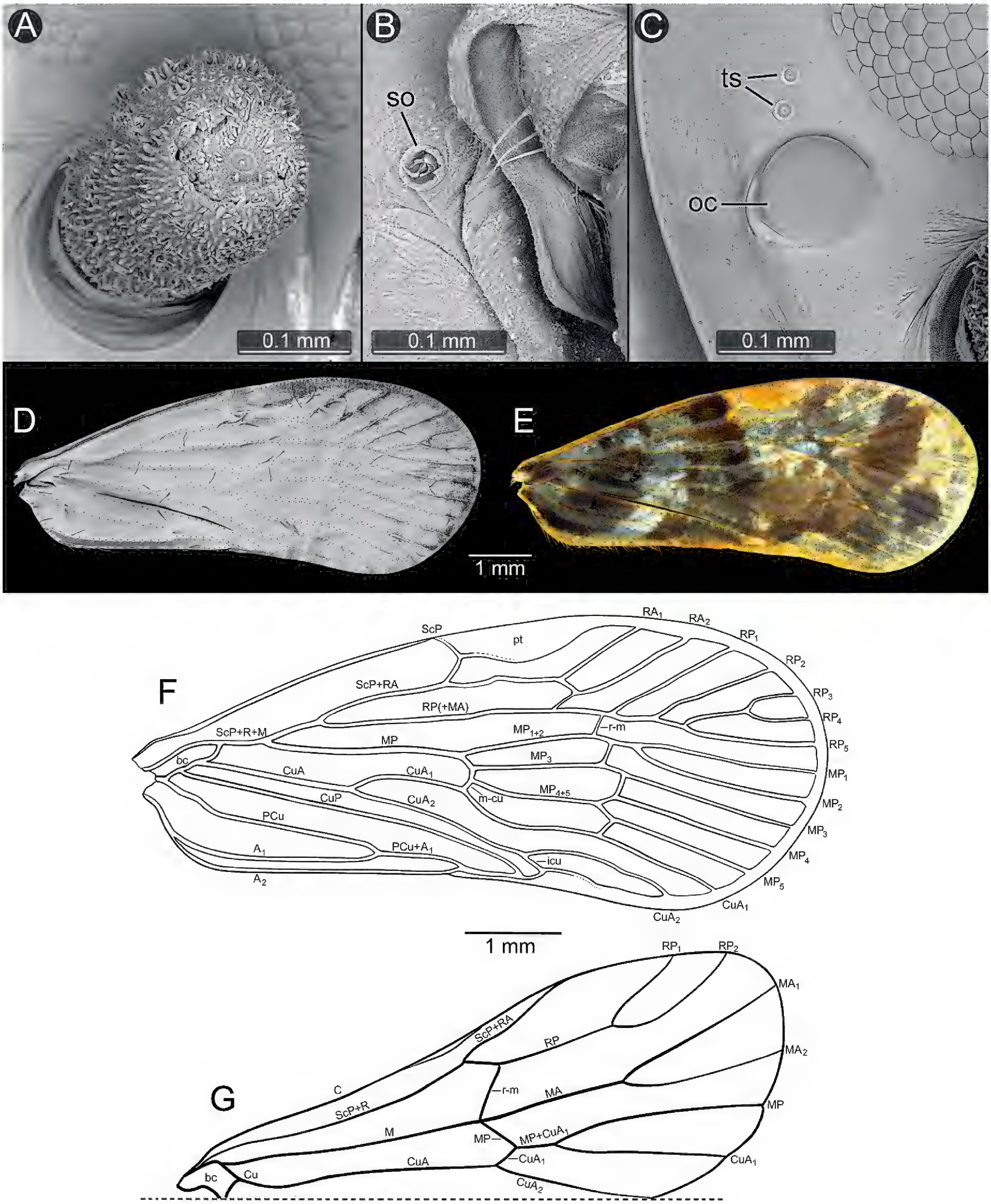

Fig. 3. *Brixiola perinetana* gen. et sp. nov., Walczak, Gębicki & Taszakowski, SEM detail of morphology. **A**. The apical part of the pedicel, top view (flagellum on both antennae broken off). **B**. Sensory organ with a complex structure on gene. **C**. Two sockets of sensory organs above ocelli. **D**. Forewing. **E**. Forewing, photo in colour. **F**. Forewing, drawing. **G**. Hindwing, drawing (visible part). Abbreviations: A = Anal vein (A_1–A_2); bc = basal cell; C = Costa vein; Cu = Cubitus vein; CuA = Cubitus anterior vein (CuA_1–CuA_2); CuP = Cubitus posterior vein; icu, m-cu and r-m = transverse venation; M = Media vein; MA = Media anterior vein; MP = Media posterior vein (MP_1–MP_5); oc = ocelli; PCu = Postcubitus vein; pt = pterostigma; Sc = Subcosta vein; ScP = Subcosta posterior vein; R = Radius vein (R_1–R_2); RA = Radius anterior vein (RA_1–RA_2); RP = Radius posterior vein (RP_1–RP_5); so = sensory organ with complex structure; ts = two sockets of sensory organs.

vertex and a narrow apical part of frons framed with high lateral carinae, which differs it from Australian endemics that possess a much shorter head. The width of the vertex (at its base) clearly exceeds its height in the genus *Innobindus*, while in *Solonaima* the vertex is at least three times and in *Undarana* even six times wider than its height (Kirkaldy 1906; Jacobi 1928; Hoch & Howarth 1989).

African species of the genus *Caffrocixius* are clearly distinguished from other genera of the tribe Brixiini, by wide and flattened frons lacking high lateral carinae, whereas *Typhlobrixia* is characterised by the reduction of compound eyes and hypogeic habitat (Synave 1953; Fennah 1967; Van Stalle 1987). The oriental genus *Melandeva* is characterised by different morphological features, including a mesonotum with five carinae (there are three carinae in *Brixiola* gen. nov.) and forewings with increased number (7) of MP branches (the first forking of MP is its division into $MP_{1+2+3+4}$ and MP_{5+6+7} branches) (Distant 1906; Emeljanov 2007). Representatives of the genera *Caffrocixius* and *Solonaima* possess a similarly characteristic structure of the mesonotum (Kirkaldy 1906; Fennah 1967; Van Stalle 1987). The genus *Cibrica* is unique by its forewing venation pattern, with MP forking into MP_{1+2+3} and MP_{4+5} branches (MP_{1+2} and MP_3 and MP_{4+5} in *Brixiola* gen. nov.). The head morphology in the genus *Brixiola* gen. nov. is similar to the genera *Cibrica* and *Brixidia* Haglund, 1899 (Haglund 1899; Holzinger et al. 2002; Emeljanov 2007). These three genera possess a narrow and laterally flattened head with deeply concave vertex surrounded by raised ridges and frons framed with foliate lateral carinae not merging in the middle of the apical part of frons. The genus *Brixidia* is identified by apical cells of tegmina considerably longer than subapical cells and CuA and icu (long and oblique) forking clearly above the apex of the clavus. Species of the genus *Brixia* may be identified by the presence of lateral carinae fused in the apical part of frons and forming of the short median groove between them. The apical part of the head formed this way has a different length in species of the genus *Brixia* (Williams 1975).

Small basal concavity of the basal part of the costal margin of tegmina has been indicated as a characteristic feature of the genus *Brixia* (Ceotto & Bourgoin 2008), but it is also present in other representatives of Cixiini, i.e., *Borbonomyndus* Attié, Bourgoin & Bonfils, 2002 assigned to the tribe Oecleini Muir, 1922 and *Eucarpia* Walker, 1857 assigned to the tribe Eucarpiini Emeljanov, 2002 (Walker 1857; Muir 1922; Attié et al. 2002; Emeljanov 2002; Holzinger et al. 2002; Tsaur & Hsu 2003; Löcker et al. 2010). Therefore, this feature cannot be considered as characteristic of the genus *Brixia*. Basal concavity is absent in *Brixiola* gen. nov.

In the hindwings, characteristic connection of r-m with M at the point where MP separating from M is present also in the representatives of genera *Pintalia* Stål (Pintallini), *Andes* Stål (Andini) and *Brixidia* (Brixidiini) of subfamily Cixiinae and *Bothriocera* Burmeister of subfamily Bothriocerinae (Emeljanov 2002). In many representatives of these genera there is a vestigial section of M at the point where r-m is connected to M vein (e.g., in *Pintalia* and *Brixidia*).

The characteristic feature of *Brixiola* gen. nov. is the presence of arched RP_1 and RP_2 reaching the costal margin. Both RP_1 and RP_2 reach apical or distal margin of the hindwing in most representatives of the Cixiinae. In *Brixidia* the venation pattern is similar to that in *Brixiola* gen. nov. with characteristic pattern of radial veins (very short RP_1 is connected with anterior wing margin, while straight RP_2 is connected with apical wing margin). The poor condition of the holotype makes it impossible to describe all features of the hindwings, especially their apical and jugal parts.

The genus *Brixiola* gen. nov. is the most morphologically similar to the genus *Brixia* (including Madagascan species). The features that distinguish these genera are summarized in Table 1.

Brixiola perinetana Walczak, Gębicki & Taszakowski gen. et sp. nov.
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(Figs 1–4)

Diagnosis

See generic diagnosis.

Description. Medium-sized species. Measurements of morphological structures are presented in table 1. Vertex trapezoidal. Frontal and lateral carinae do not merge at the top of the head. Frons without spots. Head uniformly dark-yellow. Labrum uniformly light-yellow. Pedicellus dark-yellow. Pronotum uniformly dark-brown, mesonotum with dark sides and the light central disc between lateral carinae, margins darker. Legs pale with dark-yellow, in some places, pink ridges (Figs 1A–B). Wing background hyaline with three brown bands and apical spots. In the forewing, costal margin, pterostigma and inner margin of clavus yellow. Ends of longitudinal veins yellow. The colour pattern of the wing irregularly spotted (Figs 1A, 3E). Between MP_{1+2} and MP_{3+4+5} round, brown spot. The vicinity of basal cell dark-brown. Longitudinal veins with yellowish setae embedded on pale tubercles. On light forewing background, three brown bands and one apical round spot. Hindwing milky-white with dark-brown longitudinal veins (Figs 1A–B, 3E). Sternites paler at the base, with a light-orange middle part and red margins. Ventral crest of periandrium round. Periandrium with four spines, flagellum with one long spine (Figs 4A–B).

Measurements. BODY: total length (with forewings): 8.41. HEAD: Frontal part length (including vertex + frons + clypeus): 2.32, frons length in midline: 1.13, frons total

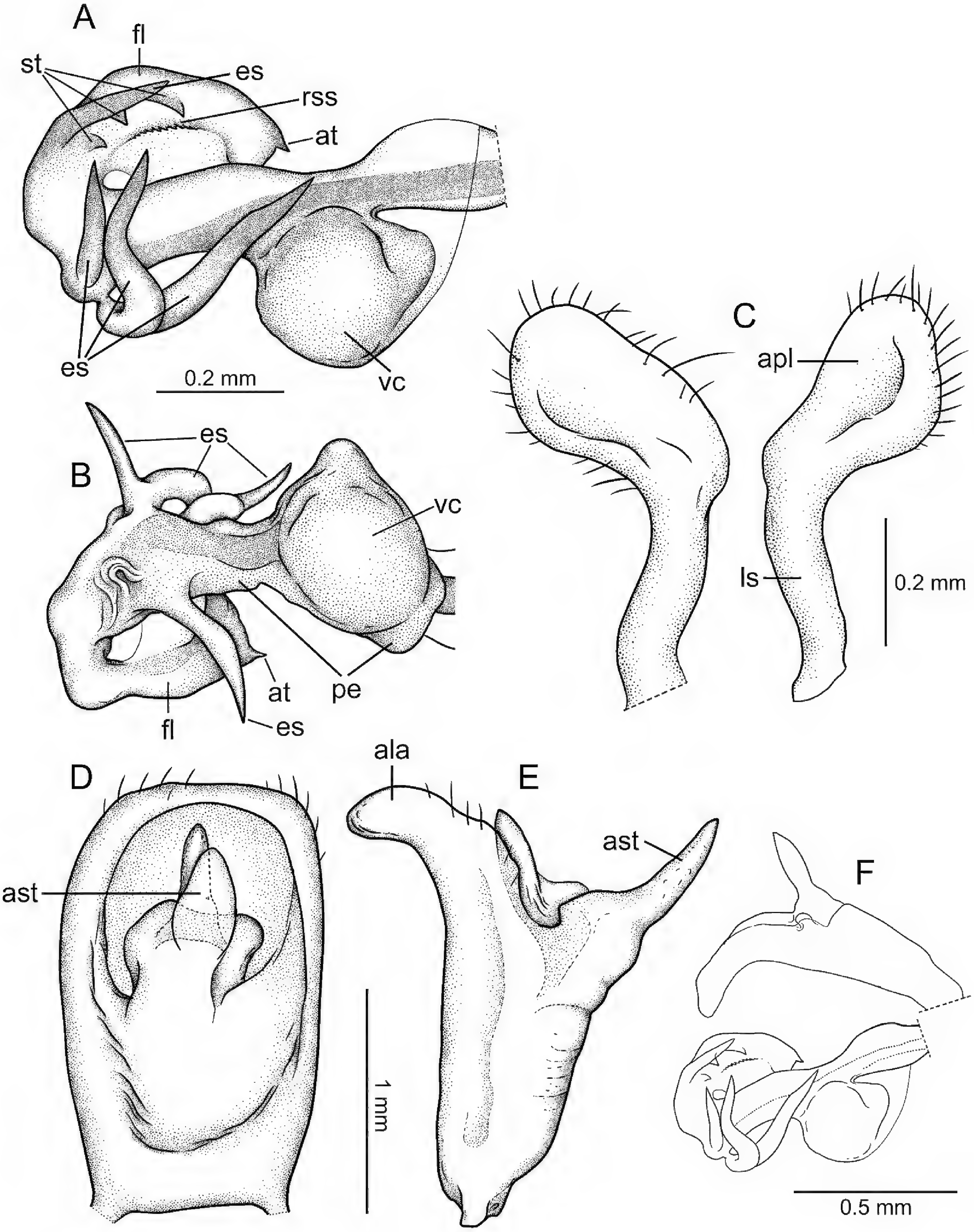

Fig. 4. Brixiola perinetana gen. et sp. nov., Walczak, Gębicki & Taszakowski, male genitalia. A. Aedeagus, side view. B. Aedeagus, ventral view. C. Styles, frontal view. D. Anal segment, dorsal view. E. Anal segment, side view. F. Laying of the anal segment with the aedeagus before preparation. Abbreviations: ala = apical lobe of anal segment; apl = apical lobes of paramere; at = apical teeth; es = elongated spines; fl = flagellum; ls = long stem; ast = anal style; pe = periandrium; rss = row of small spines; vc =, ventral crest of periandrium.

length: 1.41, frons width: 0.50, interocular distance 0.85, vertex in midline: 0.32, vertex total length: 0.39, vertex width: 0.27, eye maximum width: 0.58, clypeus maximum length in midline: 1.07, clypeus maximum width: 0.36, pedicel length: 0.37, pedicel width: 0.21. PRONOTUM: length in midline: 0.09, total length: 1.47, width: 1.76. MESONOTUM: length in midline: 1.29, width (without tegulae): 1.36. HIND LEG: femur: 1.37, tibia: 3.38, tarsus: 1.59, tarsomere: I: 1.01, tarsomere II: 0.61, tarsomere III: 0.44. FOREWING: length: 7.35, width: 3.05.

Distribution. Madagascar; species known from one locality in the eastern part of the island.

Material examined. *Holotype*, 1♂: "Holotype // *Brixiola perinetana* // gen. *et* sp. nov. // Walczak, Gębicki & Taszakowski / det. 2022" [red label] [bold font]; "MADAGASCAR Tam. // Perinet // 28.IX.58 F. Keiser" [bright pinkish label]; "Licht- // fang" [bluish-greenish label]; "♂" [dirty white label]; "H. Synave det. 1964 [64 is hand-written] // *Brixia* nov. sp." [handwritten] [dirty white label]. Examined material is deposited in the collection of the Naturhistorisches Museum, Basel, Switzerland (NHMB).

Ecology. Unknown.

Etymology. The name refers to Perinet, the place where the specimens were collected. Perinet is situated about 60 km from Antananarivo (Eastern Madagascar, near Moramanga in the vicinity of the Andasibe-Mantadia National Park).

Remarks. *Brixiola perinetana* gen. et sp. nov. is similar in body colouration to some representatives of the genus *Brixia*, especially to *Brixia trifasciata* Synave, 1956. *Brixiola perinetana* gen. et sp. nov. differs from *B. trifasciata* in having clearly uniform pale face, dark brown pronotum and a different arrangement of three fuscous stripes on the forewings (Synave 1956). *Brixiola perinetana* gen. et sp. nov. possesses two thicker anterior stripes, and one of them adheres directly to the pterostigma. The third stripe is only partially developed (reaching only MP) and is located on the apical area of the forewing. *Brixiola perinetana* gen. et sp. nov. differs from the similar species *Brixia pullomaculata* Lallemand & Synave, 1954 in having a considerably narrower and straight third stripe not reaching the apex of the forewing and the presence of a fuscous apical spot (Lallemand & Synave 1954).

Key to the African genera of the tribe Brixinii Stål, 1856

The present identification key to the African genera of the tribe Brixinii is based on external morphological characters.

1. Compound eyes reduced, frontal ocellus absent, lateral ocelli partly reduced (diminished). Tegminae with ScP and R forming a common basal stem (ScP+R); MP arises directly from basal cell .... ***Typhlobrixia*** Synave, 1953
- Compound eyes well developed (spherical). Three ocelli present. Tegminae with ScP, R and MP arising from basal cell as a common stem (ScP+R+MP) ... 2

2. Head broad, posterior part the same width as compound eye (in dorsal view), the length of its dorsal part about equal to the width (at the base of the head). Lateral carinae of vertex and frons not foliate, frons flat and broad, elliptical; long median groove reaching median ocellus. Mesonotum with five carinae (pair of submedian carinae significantly shorter than lateral pair) .... ***Caffrocixius*** Fennah, 1967
- Head narrow and slightly elongated, considerably narrower than compound eye (in dorsal view), the length of its dorsal part greater than width (at the base of the head), carinae at least partly foliate. Frons elongated, significantly narrower in its apical part, more or less concave. Median groove absent or present only in the narrowest upper part of head. Mesonotum with three carinae (submedian carinae absent) 3

3. Lateral carinae in the apex of head completely fused, forming narrow interocular part. Median groove of frons short, not reaching median ocellus ***Brixia*** Stål, 1856
- Lateral carinae of the frontal part of head broad, not fused. Frons elongately concave. Median groove of frons absent 4

4. Vein MP forking into MP_{1+2} and MP_{3+4+5}. Hind tibiae with short spines......................... ***Brixiola*** gen. nov.
- Vein MP forking into MP_{1+2+3} and MP_{4+5}. Hind tibiae without short spines........... ***Cibrica*** Emeljanov, 2007

DISCUSSION

Comparative studies on the morphology of species of the tribe Brixiini, especially the species of the genus *Brixia*, have not been conducted so far. The large genus *Brixia* exhibits a remarkable morphological diversity. The descriptions of species of the genus *Brixia* are often not precise, especially those in the old publications. The designation of groups within *Brixia* is based almost entirely on colouration, particularly wing colouration, which makes it difficult, and in many cases impossible, to confirm or correct the descriptions of many species. The genus *Brixia* needs a thorough revision, and we would not be surprised that after a comprehensive study of the Madagascan taxa, some species currently in *Brixia* are moved to *Brixiola* gen. nov. Considering the literature data, it seems possible that the Madagascan species *Brixia pullomaculata* Synave, 1956 belongs to *Brixiola* gen. nov., evidenced by the morphology of the frontal part of the head (Synave 1956).

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